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ALKWERTATHERIUM WEBBI, A NEW ZYGOMATURINE GENUS AND SPECIES FROM THE LATE MIOCENE ALCOOTA LOCAL FAUNA, NORTHERN TERRITORY (MARSUPIALIA: DIPROTODONTIDAE).

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ABSTRACT

Alkwertatherium webbi, gen. et sp. nov., possesses characteristics structurally intermediate between the diprotodontine genus *Pyramios* and the zygomaturine genus *Plaisiodon* of the family Diprotodontidae. In its expression of a clearly differentiated and well-developed parastyle on the P^3, *Alkwertatherium* is aligned with the Subfamily Zygomaturinae. In its absence of a hypocone on the P^3 and its markedly constricted diastemal palate, *Alkwertatherium* resembles the members of the Subfamily Diprotodontinae. *Alkwertatherium* was derived from diprotodontines at a structural grade similar to that of *Pyramios*. It may have shared ancestry with the primitive zygomaturines *Plaisiodon* and *Nimbadon*. *Pyramios*, *Alkwertatherium* and *Plaisiodon* exemplify a gradual structural succession in cheek tooth and cranial morphology from the Diprotodontinae to the Zygomaturinae.

KEYWORDS: Late Miocene marsupials, Alcoota Local fauna, Diprotodontidae, zygomaturinae, zygomaturine origins, Diprotodontinae, nototheriines, *Pyramios*, *Plaisiodon*.

INTRODUCTION

Primarily a description of a new taxon, this study also attempts to address the character states of the Diprotodontidae in relation to *Alkwertatherium*, which is compared with other Cheltenhamian-Mitchellian equivalent forms in considerable detail, incorporating a brief review of the mid- to late Miocene diprotodontid genera.

At least three large genera and one smaller diprotodontid genus are present in the Alcoota Local Fauna. The molar dentitions of the three largest genera: *Pyramios alcootense* Woodburne, *Plaisiodon centralis* Woodburne and *Alkwertatherium webbi*, gen. et sp. nov., overlap in size and morphology. Isolated molars of these genera are difficult to discriminate without the associated third premolar. It is possible, judging from the size distributions, that the tables of measurements provided by Woodburne (1967a) may contain an admixture of these forms. Sampling of the Alcoota site between 1985 and 1989 indicates that *Pyramios* and *Alkwertatherium* are uncommon and therefore the inclusion of the odd molar of these species would not seriously influence the statistical definition of *Plaisiodon*.

The upper third premolars of three of the four Alcoota genera are readily distinguishable.

The P^3 of *Pyramios alcootense* is characterized in having a weakly expressed or absent parastyle, absence of a hypocone and presence of a faint posterobuccal cingulum. Its broadly trilobate occlusal profile, large, conical protocone and equally large triangular, undivided parametacone with a short, steeply descending postparametacrista are associated with diprotodontine (Diprotodontinae) diprotodontids. The large size of the P^3 relative to the molars is more in proportion with the condition in zygomaturines. In Plio- Pleistocene diprotodontines, (eg. *Euryzygoma*, *Nototherium* and *Diprotodon*) the P^3 is reduced relative to the molars.

Plaisiodon centralis permanent upper premolars are elongated, with a prominent, posteriorly curved parastyle and a long, bladelike postparametacrista. The posterobuccal cingulum is absent. The hypocone is at least incipiently present, sometimes budding off the posterior side of the protocone. In some individuals the parametacone is weakly differentiated into two conjoined cusps, but the conspicuous vertical buccal sulcus that accompanies such a division in the zygomaturines *Kolopsis torus* Woodburne and *Zygomaturus* species is less distinct. *Kolopsis torus* has a broad, low molariform, 5-cusped P^3 with a divided parametacone, well-developed anterobuccal and posterobuccal cingulae and a low, but distinct mesostyle.

While these three genera cannot be mistaken for any other diprotodontid, *Alkwertatherium webbi* upper third premolars have a large parastyle combined with a *Pyramios*-like absence of the hypocone; steep, triangular undivided parametacone and large conical protocone. A weak posterobuccal cingulum is present. An indistinct mesostyle is confluent at its apex with the parametacone, as in *Pyramios*. The premolar is similar to that of *Pyramios*, but larger relative to the molars, and distinctive in its possession of a massive, strongly differentiated parastyle.

The apparent absence of unambiguous descriminative features in the upper molar dentitions and the diprotodontine-zygomaturine continuity in the premolar morphology resulting from the discovery of *Alkwertatherium* raises some issues in diprotodontid systematics. On the basis of cranial characters, *Alkwertatherium* is very similar to *Plaisiodon*, but otherwise expresses affinities with *Pyramios*.

Abbreviations of museum accession numbers: NTM, Northern Territory Museum; NMV, Museum of Victoria (formerly National Museum of Victoria); CPC, Commonwealth Palaeontological Collection (BMR); SGM, Spencer and Gillen Museum (NTM Alice Springs); VCMP, University of California Museum of Paleontology.

SYSTEMATICS

Family Diprotodontidae Gill
Subfamily Zygomaturinae Stirton, Woodburne and Plane

Genus *Alkwertatherium* gen. nov.

Type species. *Alkwertatherium webbi* sp. nov.

Diagnosis. Cranium narrower (relatively longer in proportion to width) than *Pyramios*, *Plaisiodon*, *Kolopis* or *Neohelos*; dorsal profile forming a distinct vertex, with weak frontal and low sagittal crests resembling the type *Plaisiodon centralis* (CPC 6784). Constricted and elongated postsquamosal lamina, similar to, but more extreme than in *Neohelos* or *Plaisiodon*; occiput lower and narrower than any similar-sized diprotodontid. Rostrum narrower than in *Pyramios*, *Plaisiodon* and *Neohelos*, constricted at the level of the infraorbital foramen; diastemal palate similar to, though longer and more narrowly constricted immediately anterior to P^3 than in *Pyramios*; laterally expanded premaxillary palate, as in *Pyramios*, but with a shallow, wide, as opposed to a narrow, deep, interincisival fossa. Nasals elevated slightly and expanded anteriorly as in *Plaisiodon* and *Neohelos*, not downturned and pointed as in *Pyramios*. Zygomatic arch long, as deep anteriorly as posteriorly, contrasting with the short, anteriorly narrowing zygomatic arches of *Pyramios*. Squamosal-jugal suture long, squamosal process extends to beneath the orbit as in *Pyramios*; contour of arch relatively flat as in *Plaisiodon* and in contrast to the strongly-bowed zygomatics of *Pyramios*; masseteric processes broad and short as in *Neohelos*, in contrast to long, robust processes in *Pyramios*; deep, well-defined nasolabialis fossa similar to *Plaisiodon* and *Neohelos*, but differing from *Pyramios* in which the fossa is poorly developed. Trilobate, posteriorly broad P^3 composed of a large, slightly buccally offset parastyle, pyramidal, undivided parametacone and conical protocone; hypocone absent, weak posterobuccal cingulum present, differing from *Pyramios* in having a well-developed parastyle as large or larger than that of *Plaisiodon*. Upper molars more similar to *Pyramios* than to *Plaisiodon* with gradual progression in molar width from M^{2-4}; wide interproximal contact between P^3 and M^2, but differing from *Pyramios* in having a more distinct, thicker lingual cingulum, wider mouth of the lingual side of the interloph sulcus, more concave posterior surface of the hypoloph, more distinct "midlink", large metastyle on M^4 and much narrower hypoloph on M^5. A conspicuous obliquity of the lophs of M^{2-3} resembles the condition of later diprotodontines, but *Plaisiodon* among the zygomaturines, has similarly obliquity of the lophs. Dentary hori-

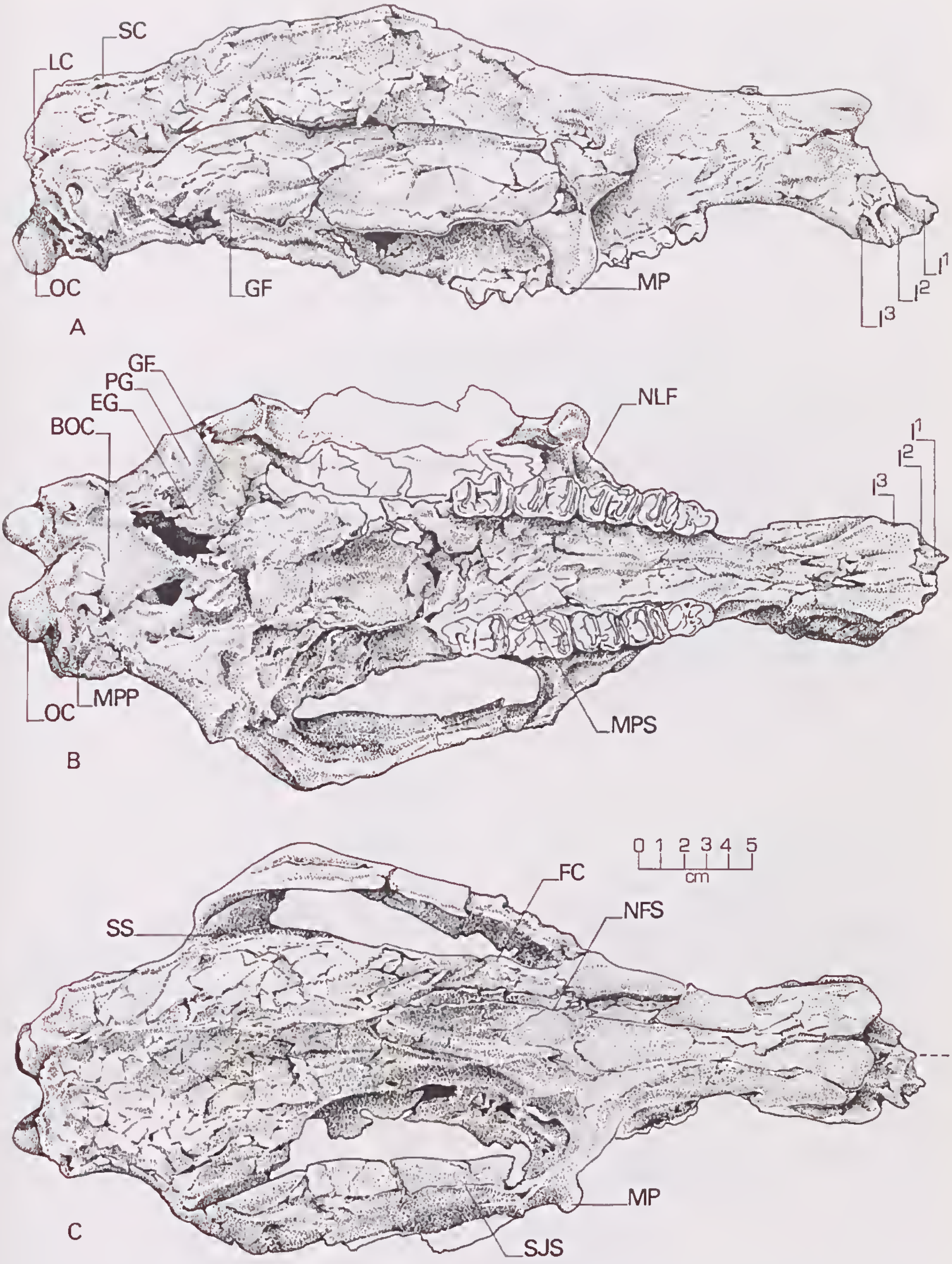

Fig. 1. *Alkwertatherium webbi* gen. et sp. nov. (holotype, SGM 888). **A,** lateral aspect of cranium; **B,** ventral aspect of cranium; **C,** dorsal aspect of cranium. Abbreviations: **LC**, lambdoid crest; **OC**, occipital condyle; **GF**, glenoid fossa; **MP**, masseteric process; **In**, incisors; **BOC**, basioccipital; **EG**, entoglenoid swelling; **PG**, postglenoid process; **NLF**, nasolabial fossa; **MPP**, mastoid/paroccipital process; **MPS**, maxillo-palatine suture; **FC**, frontal crest; **NFS**, nasofrontal suture; **SC**, sagittal crest; **SS**, squamosal sulcus; **SJS**, squamosal-jugal suture.

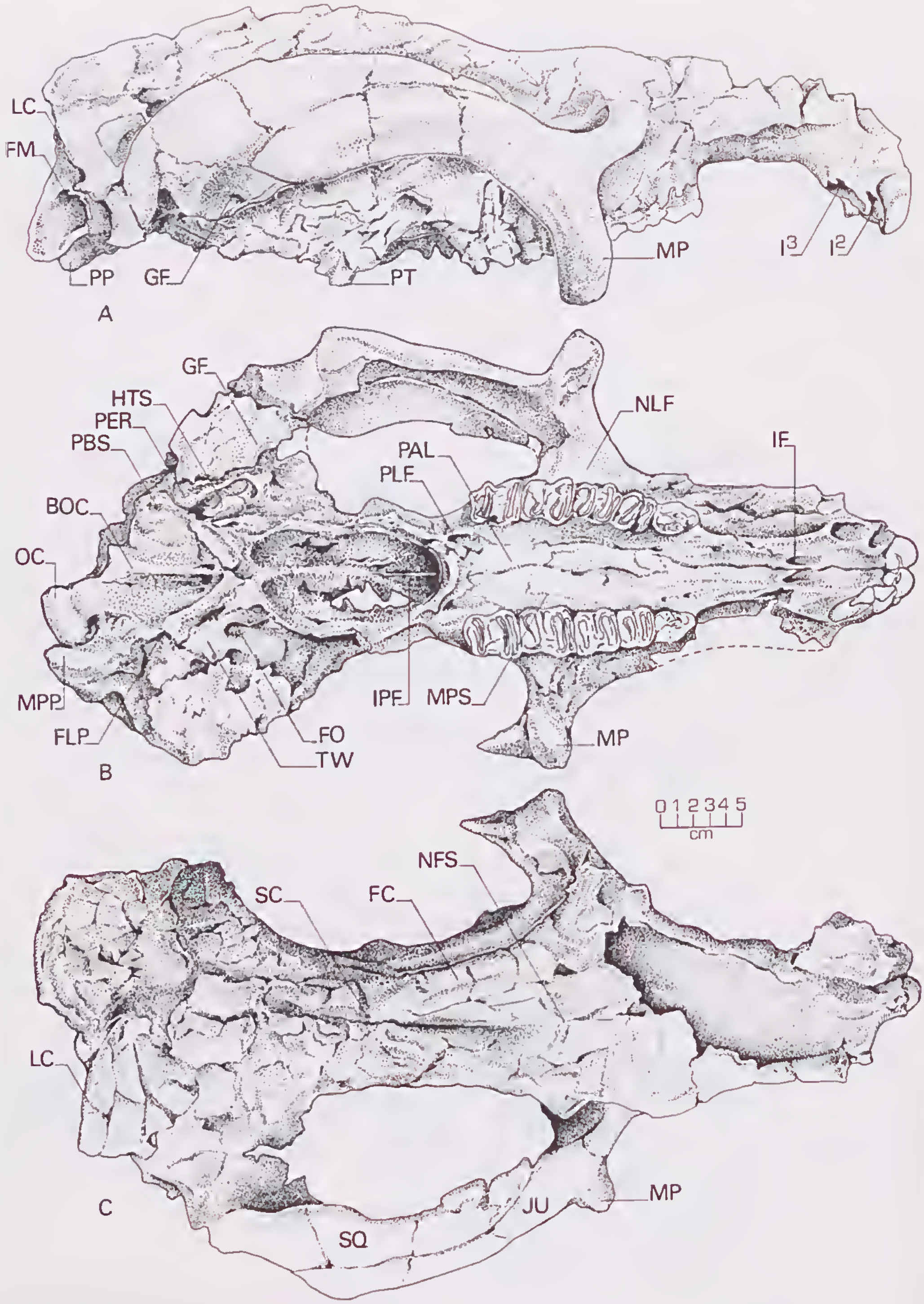

Fig. 2. *Plaisiodon centralis* Woodburne, 1967 (SGM 871) for comparison with *Alkwertatherium webbi*. **A**, lateral aspect of cranium; **B**, ventral aspect of cranium; **C**, dorsal aspect of cranium. Abbreviations not included in Fig. 1: **FM**, foramen magnum; **PP**, paroccipital process; **PT**, pterygoid; **HTS**, breached hypotympanic sinus; **PER**, periotic; **PBS**, paroccipital-basioccipital suture; **FLP**, foramen lacerum posterior; **TW**, vestigial squamosal tympanic wing; **IPF**, interpterygoid fossa; **PLF**, posterolateral palatine foramina; **PAL**, palatine; **IF**, incisive foramina; **SQ**, squamosal; **JU**, jugal.

zontal ramus deep but relatively thin in section, inferior border straight and proportionally similar to *Plaisiodon*; differing from the short, deep, thick-sectioned ramus with convex "rocker" inferior border profile of *Pyramios*; straight, strong, high diastemal crests expanded into wide, flattened surfaces anteriorly and elongated diastema resembling *Plaisiodon* proportionally but more similar to *Pyramios* in its expression; dentaries unankylosed at the symphysis as in *Plaisiodon* and in contrast to *Pyramios*; symphysis extremely long and horizontal, extending to posterior M_2, as opposed to *Pyramios* in which the symphysis is short and steeply inclined. Sublingual fossa long, narrow and horizontal, similar to *Plaisiodon*, much longer and more horizontal than in *Pyramios*; lower incisor crowns wide, thick, and spatulate, resembling those of *Pyramios* and the New Guinea Pliocene zygomaturine, *Kolopsoides*.

Etymology. *Alkwerta* (= *Alcoota*) means "native shield" in Eastern Arrente or Iliaura language. *Alkwerta* is the accepted Arrente orthography of *Alcoota*. The area around Alcoota Homestead was named after a rocky landmark resembling a shield. As this object is similar in shape to the parastyle of the upper third premolar, reference is made to the prominence of the cusp which appears to stand up in front of the tooth like a shield. The generic name *Alkwertatherium* also emphasizes the uniqueness of the Alcoota Local Fauna by designating a form with the locality name.

Alkwertatherium webbi n.sp
(Figs 1-13)

"Plaisiodon" webbi Murray, 1989:12 (nomen nudem).

Type material. HOLOTYPE - SGM 888: nearly complete, slightly crushed and asymmetrically distorted cranium missing the incisors, paroccipital processes and portions of the basicranium. PARATYPES - SGM 883: associated dentaries missing third premolars and posterior portion of the ascending rami. SGM P892: right dentary fragment with with complete cheek dentition (P_3-M_5).

Comparative material. *Plaisiodon centralis* - SGM 887: maxillary palate; SGM 881: right dentary; SGM 772: right dentary fragment; SGM 885: left maxillary fragment with complete cheek dentition; SGM 884: cast of holotype (CPC 6784); SGM 871: cranium. *Pyramios alcootense* - SGM 872: palate with complete right cheek dentition. *Neohelos tirarensis* - SGM 891: right and left dentaries from cranium of NTM P8695-38. *Kolopsis torus* - SGM 889: cranium. Supplementary specimens referred to are noted in the text and figures.

Diagnosis. As for the genus.

Type Locality. Alcoota, Flinders Quarry, "...Waite Formation, 4 miles [6.4 km] southwest of Alcoota Station, 2.1 miles [3.4 km] southwest of junction of Waite and Ongeva Creeks, Northern Territory, Australia" (Woodburne 1967b).

Age. The Alcoota Local Fauna is probably Cheltenhamian Stage equivalent or slightly older (Woodburne *et al.* 1985). *Kolopsis* sp. and *Zygomaturus gilli* are reported from Beaumaris, Victoria which is considered to be Cheltenhamian Stage (Stirton *et al.* 1967). A *Kolopsis* species (*Kolopsis rotundus* Plane) is described from the radiometrically dated Otibanda Formation of New Guinea, at between 7.6-5.7 million years B.P. (Evernden *et al.* 1964; Stirton *et al.* 1967). That age has subsequently been adjusted to between 3.5 and 2.5 myBP (Page and McDougall 1972; Hock and Holm 1986). Stirton *et al.* (1967) consider the Awe Fauna to be a relict of mid-Tertiary Australian faunas and therefore not amenable to an overall stage of evolution correlation. On the basis of the presence of *Zygomaturus* at Beaumaris, the Alcoota Local Fauna is provisionally considered to be older than the Beaumaris Local Fauna.

Description and comparison. General comparison: The cranium of *Alkwertatherium webbi* (Fig. 1) is more similar in overall appearance to *Plaisiodon centralis* (Fig. 2) and some morphs of *Neohelos tirarensis* than it is to either *Pyramios alcootense* or *Kolopsis torus*. The *Alkwertatherium webbi* cranium is smaller, more elongated and laterally compressed, more gracile and more prognathic than any known example of *Plaisiodon centralis* or *Pyramios alcootense* (Fig. 3). The upper incisor arcade is broader and more procumbent (Figs 4-5; Tables 1-2); the rostrum is narrower and more elongated. The palate is narrower and the cheektooth row is straighter, narrower and shorter (Fig 6).

The gracile, elongated *Alkwertatherium webbi* cranium is proportionally dissimilar to the type *Pyramios alcootense* (CPC 6749), (Fig. 6), which has a broad, relatively short

Table 1. Measurements (mm) of A, upper incisors, B, lower incisor, including implantation angles, and C, dentary dimensions.

A. UPPER INCISORS

	Alveolar length		implantation angle	
	A. webbi	*P centralis*	*A. webbi*	*P. centralis*
I^3	14.5	20.6	145°	130°
I^2	10.6	10.8	145°	115°
I^1	15.0	16.5	175°	150°

B. LOWER INCISOR

	Thickness	Width	Implantation angle (frontal, from horizontal)
A. webbi	11.0	29.0	20°
P. centralis	12.0	12.9	55°
P. alcootense	11.0	28.0	40°

C. DENTARY MEASUREMENT

	P. centralis	*A. webbi*	*P. alcootense*
Length I_1 to P_3	80.0	85.0	67.5
Length tooth row	148.5	117.0	112.2
Depth at M_4	70.0	55.5	60.0
Depth M_2/M_3	74.5	68.3	80.5
Depth at P_3	53.5	60.0	65.0
Length ramus	315.0	276.0	270.0
Length symphysis	121.0	117.0	88.0
I_1 above inferior border	52.0	23.0	50.0

cranium, long robust masseteric processes and lacks the postorbital and postsquamosal constrictions conspicuous in *A. webbi* and to a lesser extent *P. centralis*. However in certain specific features, principally those relating to the trophic complex, *Pyramios alcootense* shows some striking similarities to *Alkwertatherium*. These are seen in the narrowly constricted diastemal palate, strongly developed diastemal crests, flared premaxillary palate, broad, spatulate lower incisors and length of cheek tooth rows. There are no specific similarities to *Kolopsis torus* expressed in the cranium and dentaries of *Alkwertatherium*.

Cranium: The lateral profile of the cranium of *Alkwertatherium webbi* is long and relatively low, but with a definite vertex, unlike that of the holotype of *Plaisiodon centralis* (CPC 6784) (Fig. 1). A subsequently recovered specimen of *P. centralis* (SGM 871) also differs from the holotype in this respect (Fig. 2). It is possible that the holotype represents an extreme condition for the genus *Plaisiodon*. The basicranial axis of *Alkwertatherium* is however, less upward-flexed relative to the occlusal plane than either the type specimen or SGM 871 *Plaisiodon centralis*. *Alkwertatherium webbi*'s cranium is approximately the same length and has the same state of tooth wear as the *P. centralis* type, which has the advantage of neutralizing the considerable allometric distortions encountered in this family in relation to size, growth stage, and sexual dimorphism (Table 2).

The rostrum of *Alkwertatherium webbi* is narrower, more uniformly tubular and about the same length as *P. centralis*, CPC 6784, but differs in being constricted bilaterally at the level of the infraorbital foramen, and the nasals are narrowest, about 30 mm across at this point, in relation to the arcing dorsal margin of the maxilla. Each nasal termination of *A. webbi* is gently rounded and widest there (46 mm) in contrast to *P. centralis* in which the widest point of the combined nasal bones is immediately anterior to the jugal eminence. *Pyramios* nasals are narrowest distally and combine to form a pyriform, decurved, overhanging nasal process.

Table 2. Measurements (mm) of the A, upper, and B, lower cheek dentitions of *Alkwertatherium webbi* compared with *Pyramios alcootense* and *Plaisiodon centralis*.

A. UPPER CHEEK DENTITION

	Alkwertatherium		*Pyramios*		*Plaisiodon*	
	L888	R888	L872	R872	L887	R887
P^3 L	18.7	19.2	–	18.0	24.0	23.3
W	17.7	17.6	–	17.1	17.6	17.7
M^2 L	23.3	22.5	–	20.0	23.5	23.5
AW	19.2	18.8	–	18.2	20.0	20.0
PW	18.1	18.2	–	18.0	20.0	21.0
M^3 L	27.1	25.2	–	25.2	27.1	26.5
AW	21.5	–	–	21.0	23.0	22.5
PW	–	19.7	21.2	19.0	21.6	21.1
M^4 L	28.7	27.7	26.0	26.7	32.0	30.1
AW	22.5	24.1	23.9	22.5	25.5	25.5
PW	18.3	–	20.5	21.0	22.2	–
M^5 L	27.7	–	–	28.5	–	32.0
AW	20.1	–	–	24.9	–	27.2
PW	17.0	–	–	21.0	–	19.8

B. LOWER CHEEK DENTITION

	Alkwertatherium		*Pyramios*		*Plaisiodon*	
	R892	L883	R883	L891	R891	R881
P_3 L	13.8	–	–	16.5	15.5	19.5
W	9.5	–	–	11.0	10.6	13.5
M_2 L	21.5	19.9	18.3	20.6	20.3	24.0
AW	14.5	14.0	–	14.3	15.2	15.2
PW	15.0	15.1	13.7	15.0	14.4	17.0
M_3 L	26.2	23.9	22.1	–	–	30.5
AW	19.0	17.3	15.5	17.0	18.5	19.0
PW	–	–	14.8	–	–	19.8
M_4 L	28.2	25.5	25.8	28.0	27.5	35.0
AW	20.2	18.7	–	20.5	20.0	23.0
PW	18.3	–	18.3	18.8	19.0	23.0
M_5 L	26.2	27.5	27.4	30.0	30.0	33.2
AW	19.5	20.5	20.3	20.4	21.0	24.9
PW	16.6	17.8	18.2	19.2	19.0	21.5

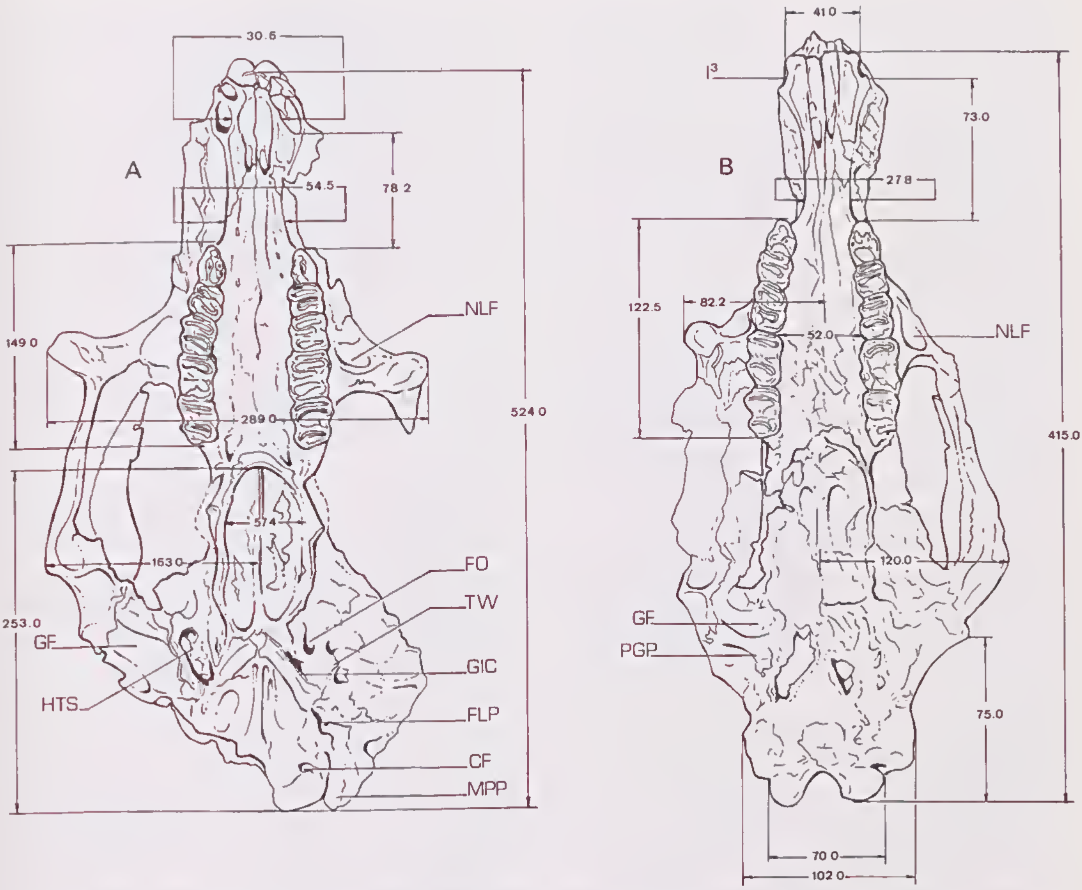

Fig. 3. Dimensions and comparison of the ventral aspect of *Alkwertatherium webbi* with *Plaisiodon centralis*. **A**, *Plaisiodon centralis* (SGM 871); **B**, *Alkwertatherium webbi* (SGM 888). Key to abbreviations (see Figs 1-2), plus: **GIC**, groove for internal carotid artery; **FO**, foramen ovale; **CF**, condylar foramen. Scaled to equivalent condylobasal length.

In lateral view, the profile of the diastema is slightly more elongated and less curved downwards along with the profile of the incisors than in *P. centralis* (Fig. 5). As in *P. centralis*, the premaxillary-maxillary suture is nearly vertical. The dorsal profile of the nasals is gently concave. Though slightly crushed, a natural-looking depression located about 30 mm behind the end of the nasals indicates that they were weakly elevated. A small premaxillary-nasal notch appears to have been present. The narial aperture is trapezoidal, the nasals lying almost horizontal to the frontal plane. Posteriorly, the nasal bones are gabled resulting in a low, oval elevation situated immediately anterior to the frontal depression. *Alkwertatherium* and *P. centralis* are similar in this respect, and strong resemblances to *Neohelos* are also present in the dorsolateral contours of the rostrum and particularly in the basic shape of the nasal bones.

Alkwertatherium differs substantially from *Plaisiodon* and *Pyramios* in the width of the base of the rostrum at the nasofrontal contact. In *A. webbi*, the width of this region, 50 mm, is little more than half the width of the similar-sized *Plaisiodon*, CPC 6784, and considerably less than half the width of that of *Plaisiodon*, SGM 871. Immediately behind the rostrum, *Alkwertatherium* resumes its proportional similarities with CPC 6784, in which the interorbital width is only slightly greater than that of the new genus.

The frontal region of *Alkwertatherium* retains the narrow aspect of the base of the rostrum as it ascends into the frontal crests. The frontal depression is shallow and flat compared to the deeply clefted fossae in CPC

6784 and SGM 871, *Plaisiodon centralis*. In *Pyramios alcootense* the frontal crests are large, rounded swellings in marked contrast to the long narrow, crisply delineated and straight crests of *Plaisiodon* and *Alkwertatherium*. As in *P. centralis*, the frontal crests converge in a low sagittal crest and the flat lateral wall of the braincase descends steeply towards a long, narrow squamosal sulcus. In *Pyramios* the frontal crests do not converge into a sagittal crest, remaining as separate temporalis crests for the length of the neurocranium. The basic shape of the neurocranium of *Alkwertatherium* differs little from that of *P. centralis*, except for its greater length and narrowness posterior to the squamosal root, and the extent to which it is elevated above the tooth row. The latter difference however, amounts to only about ten degrees.

A larger discrepancy in cranial shape between *Alkwertatherium webbi* and *Plaisiodon centralis* is the nasofrontal angle, which, as measured at the nasofrontal suture, registers a difference of about twenty degrees (Fig. 6). As in *P. centralis* the parietals of *Alkwertatherium* are long and narrow and the squamosal lamina is broad. The postsquamosal arch in *Alkwertatherium* is considerably longer and more deeply concave than in comparable *P. centralis* specimens.

The zygomatic arch of *Alkwertatherium webbi* is deep and long. The contour of the undistorted left zygomatic arch is flatter than in *P. centralis*, closely resembling the condition in *Neohelos tirarensis* (Fig. 6). The squamosal process is long and sustains a considerable width, extending anteriorly to lie beneath the orbit. The squamosojugal suture also contributes to the posterior orbital margin in *Pyramios*. Both CPC 6784 and SGM 871 have much shorter squamosal processes that terminate 30 mm or more posterior to the distal orbital margin. Consequently, in *Alkwertatherium*, the zygomatic arch is at least as deep anteriorly, immediately posterior to the orbit, as it is immediately anterior to the glenoid fossa.

In *P. centralis* and *Pyramios alcootense*, the zygomatic arch is narrower anteriorly than it is posteriorly. Although the squamosal process does not extend as far anteriorly in *Neohelos* as in *Alkwertatherium*, the anterior depth of the arch is approximately the same as the posterior depth, and the squamosal process is relatively longer than in either *Plaisiodon* or *Pyramios*. The masseteric process in *A. webbi* is relatively delicate and short, not extending more than a few millimetres below the occlusal line. The processes are missing from the holotype of *P. centralis* but its broken surface indicates that a much more robust process was present. The extent to which the masseteric process was developed in *P. centralis* is demonstrated by SGM 871. The masseteric processes of *Pyramios* are also much longer and more robust than in *Alkwertatherium*. The nasolabial fossa is deeper, more inferiorly directed and more sharply delineated in *Alkwertatherium* than in *Plaisiodon* or *Pyramios*, more closely resembling that of *Neohelos tirarensis*.

Palate: The diastemal palate of *Alkwertatherium webbi* is markedly constricted immediately anterior to the P^3 and attains a minimum width of only about 28 mm at 15 mm anterior to the tooth. Anterior to the P^3, at 25 mm, the palate begins to flare laterally to attain a maximum width of 52 mm immediately posterior to the I^3 alveoli. In *P. centralis*, the diastema is moderately narrow, relatively more constricted than in most *Neohelos tirarensis* and *Kolopsis torus* crania in which the maximum interincisival width is approximately the same as the interdiastemal minimum (Figs 5-6; Tables 1-2). In conjunction with the anteriorly expanded premaxillary palate, the incisor alveoli open more laterally than ventrally and the implantation angles of the incisor roots are closer to horizontal. A more graphic expression of this complex is seen in the position of the I^3 alveolus immediately in line with I^2 in *Plaisiodon centralis*, *Neohelos tirarensis* and *Kolopsis torus* in contrast to the laterally offset I^3 alveoli in *Alkwertatherium*. In the morphology of the diastemal and premaxillary palate, *Alkwertatherium* is a bit different from zygomaturines, more closely resembling the notothere *Pyramios alcootense*. However, in *Pyramios*, the interincisival fossa is a deep, spoon-shaped depression. In *Alkwertatherium*, the interincisive region is a shallow, wide concave surface.

Although no upper incisors have been identified for the species, the implantation angles of the teeth indicate that the crowns were more procumbent than in *P. centralis*, *Neohelos tirarensis* or *Kolopsis torus*. The diastemal palate is also relatively longer than in *P. cen-*

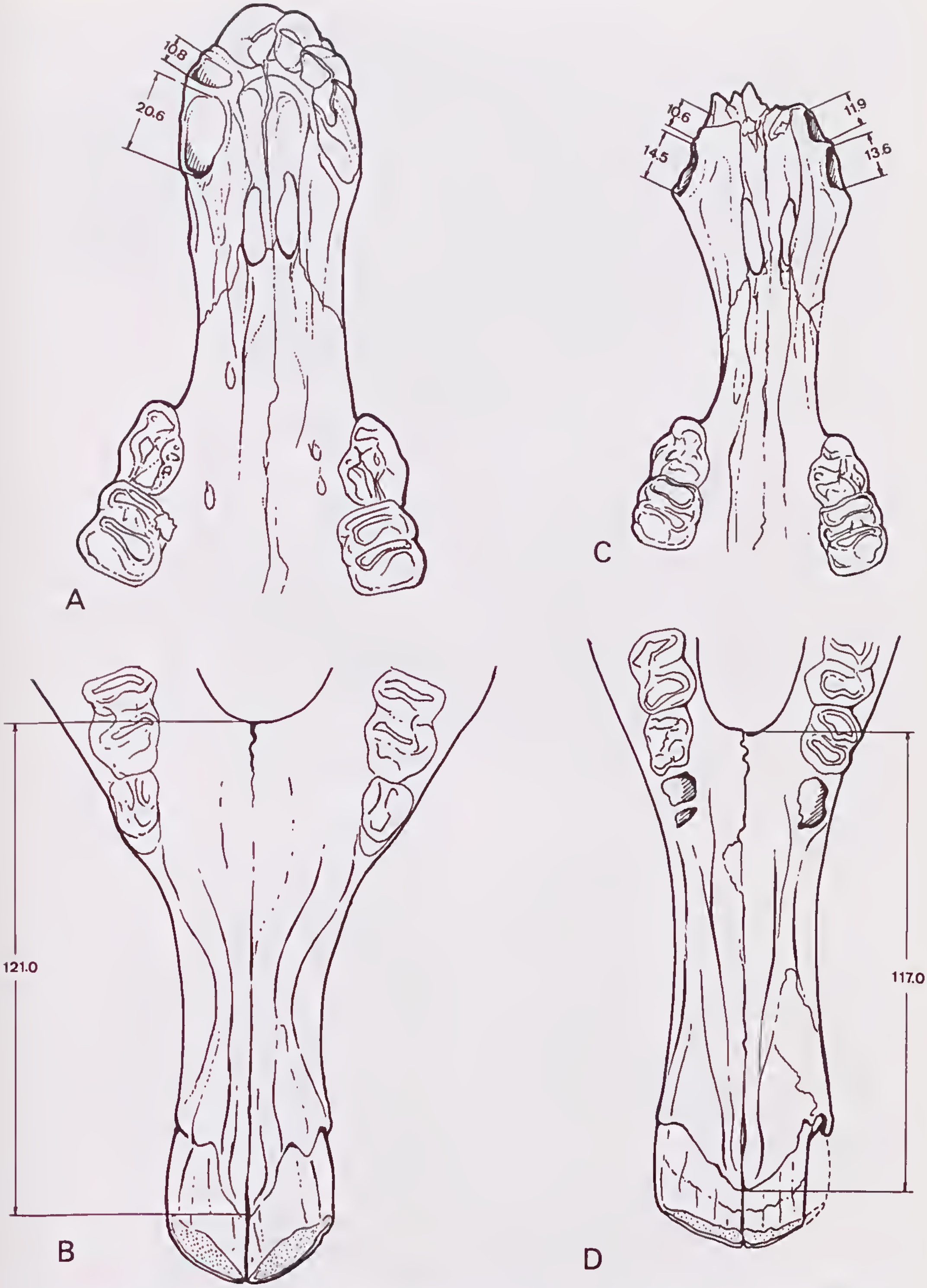

Fig. 4. Comparison of the anterior palatal and dentary diastemal regions in *Alkwertatherium webbi* and *Plaisiodon centralis*. **A**, ventral aspect of anterior palatal region of *P. centralis* (SGM 871); **B**, ventral aspect of symphysial region of the dentary of *P. centralis*; **C**, ventral aspect of anterior palatal region of *A. webbi* (SGM 888); **D**, ventral aspect of the symphysial region of the dentary of *A. webbi*. Not to scale.

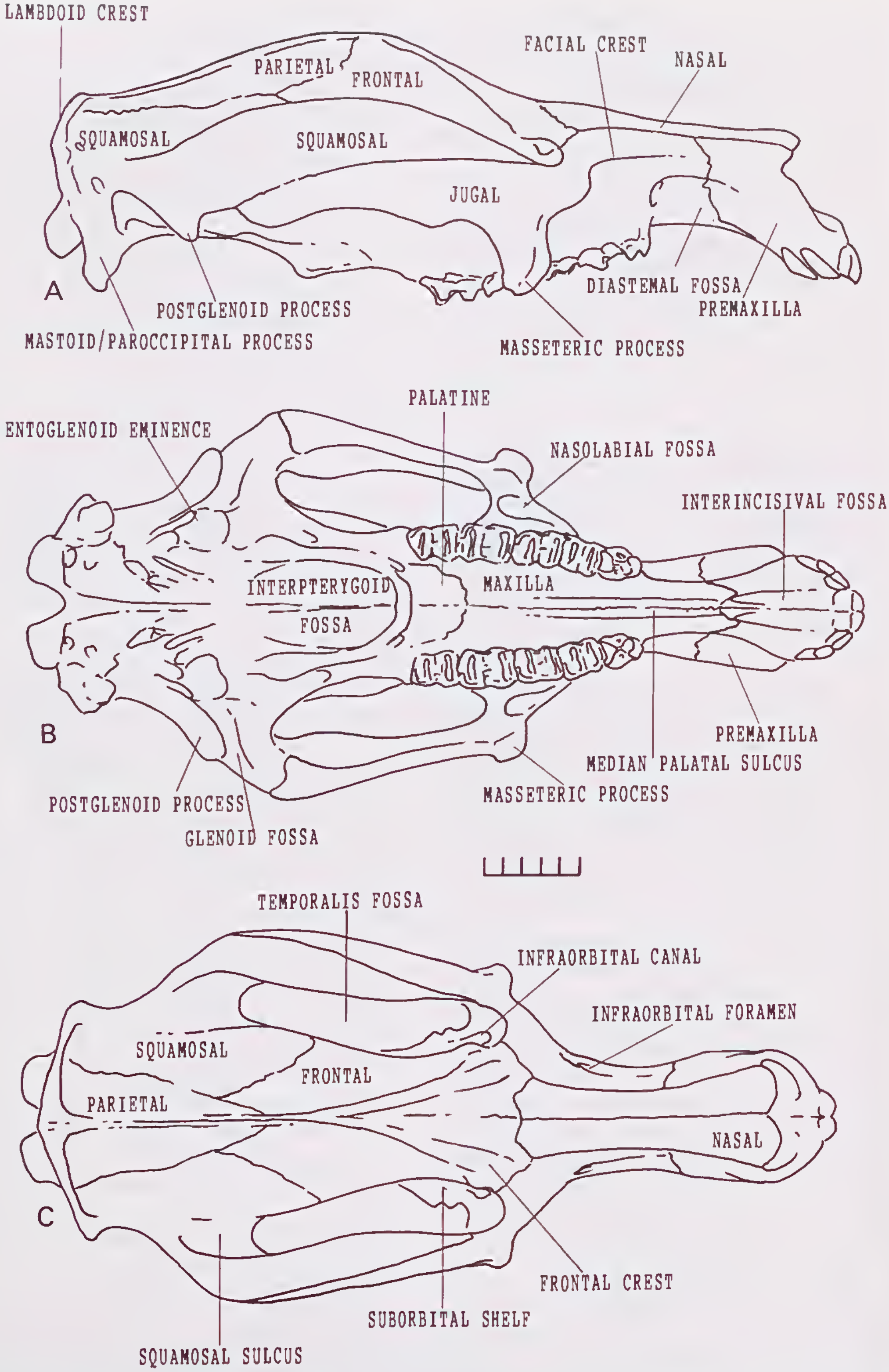

Fig. 5. Restorations of *Alkwertatherium webbi* gen. et. sp. nov. **Opposite**, restorative sketch of lateral aspect of skull, scale 50mm; **A-C**, diagrammatic restorations of cranium.

tralis. The incisor implantation in *Pyramios* is more similar to that of *Alkwertatherium*, though also less procumbent.

The maxillary palate of *Alkwertatherium* is slightly narrower than in *P. centralis*, made less visually apparent perhaps, by the narrower and shorter cheek tooth rows (Figs 1-3, 6). The palate is otherwise similar to that of *Plaisiodon*, particularly in the shape of the cheektooth arcade and moderate extent of posterior divergence. *Pyramios alcootense* has a relatively broader, shorter, more domed palate with more posteriorly divergent tooth rows (Fig. 6).

Cranial base: The internal nares and interpterygoid fossa appear to be shallower in *Alkwertatherium* than in *P. centralis*, in which an exceptionally deep, cavernous excavation is a conspicuous feature of SGM 871. The cranial base is poorly preserved in *Alkwertatherium*. Sufficient surface contour is present to define the extremely wide, obliquely oriented glenoid fossae, ventrolaterally directed pterygoid fossae and low, wide, but apparently thin, delicate postglenoid processes. SGM 871, *Plaisiodon centralis*, preserves many basicranial features of the genus and the majority of those portions visible in *Alkwertatherium* appear to correspond closely to it. In *Pyramios*, exceptionally wide glenoid fossae are oriented at right angles to the axis of the cranium. There is, moreover a highly distinctive lateral profile of the glenoid notch which is narrowly V-shaped, as opposed to the broadly U-shaped profile of *Alkwertatherium*. An interesting similarity between *Pyramios* and *Alkwertatherium* is the shared feature of thin postglenoid processes.

The occipital region of *Alkwertatherium* is conspicuously narrower than in *Plaisiodon*, *Pyramios* and *Kolopsis*, but is similar in width though lower than in some *Neohelos* specimens (eg. NTM P8695-38). The occipital condyles, which are the most posterior structures of the cranium, are comparatively small, transversely elongated and narrow, in contrast to the large, widely separated occipital condyles of *Pyramios*. The condyles are separated ventrally by a deep, V-shaped inter-

Table 3. Cranial measurements (mm) of *Alkwertatherium webbi* (888) compared with *Plaisodon centralis* (884, 871) and *Pyramios alcootense* (872).

Cranial measurements	SGM888	872	884	871
Length-I1 to occipital condyle	415.0	–	–	520.0
Length-lambdoid crest to outer I^1	–	–	–	525.0
Length-zygomatic arch	204.0	–	195.0	243.0
Length-temporalis fossa	122.0	–	125.0	155.0
Length-diastemal palate	73.0	–	52.0	78.0
Length-upper cheek tooth row	122.5	120.0	–	149.0
Length-interpterygoid fossa	–	–	–	138.0
Length-masseteric process	65.2	–	–	104.5
Length-lambdoid crest to nasals	395.0	–	–	–
Height-basioccipital-sagittal cres	70.0	–	122.0	121.0
Depth-vertex to pterygoid	145.0	–	–	175.0
Depth-posterior zygomatic arch	50.0	–	52.4	84.5
Depth-anterior zygomatic arch	50.0	–	–	56.6
Distance-molars above masseteric pr	<5.0	–	–	35.0
Depth-maxilla above P^3	57.0	–	54.0	–
Depth-from M^{4-5} to top of frontal	110.0	–	104.0	115.0
Width-occiput	98.0	–	–	130.0
Width-across mid point of orbits	95.0	–	110.0	140.0
Width-frontal above orbits	58.0	–	88.0	127.0
Width-cranium at frontal converg.	60.0	–	61.0	60.0
Width-PMX across narial aperture	69.0	–	60.0	92.0
Width-zygoma to sagittal crest	120.0	–	90.0	167.0
Width-anterior to lambdoid crest	102.0	–	–	190.0
Width-premaxillae between I^3	41.0	–	26.0	30.0
Width-palate anterior to P^3	27.8	39.0	37.7	54.5
Width-maxillae labial sides P^3	67.0	72.0	75.5	91.4
Width-palate lingual M^{1-4}	52.0	62.0	–	64.0
Width-maxillae labial sides M^5	87.0	100.0+	–	111.0
Width-interpterygoid fossa	47.0	–	–	54.0

condylar notch. The foramen magnum is transversely wide and distinctly oval in shape. Immediately above the foramen magnum, the proportionally small occipital surface was deeply excavated for the attachment of nuchal musculature.

Table 4. Summary of characters of *Alkwertatherium webbi* gen. et sp. nov. and key to comparisons shown in Figures 6, 8, 11, 13.

Summary of characteristics of *Alkwertatherium webbi*
1.0 Dorsum cranii
1.1 high steep frontal
1.2 constricted preorbitally
1.3 constricted postsquamosally
1.4 upward basicranial flexion
1.5 high, thin narrow frontal crests
1.6 anteriorly expanded nasals
1.7 trapezoidal narial aperture
1.8 low, narrow occiput
1.9 wide, oval foramen magnum
2.0 Zygomaticofacial
2.1 long, deep squamosal process of zygomatic arch
2.2 zygomatic arch flattened in lateral aspect
2.3 zygomatic arch deep anteriorly
2.4 short, delicate masseteric processes
2.5 deep, well-defined nasolabial fossa
2.6 high, distinct sinuous facial crest
2.7 long, well defined buccinator sulcus
2.8 long squamosal sulcus
2.9 shallowly arcing diastemal profile
3.0 Palate
3.1 flat, narrow and long
3.2 nearly straight arcades, slight posterior divergence
3.3 diastemal palate markedly constricted
3.4 flaring premaxillary palate, shallow IC fossa
3.5 I^3 lateral to I^2, alveoli open anterolaterallly
4.0 Basis cranii
4.1 Narrow, shallow interpterygoid fossa
4.2 small, shallow pterygoid fossae
4.3 wide oblique glenoid fossae
4.4 deep, V-shaped intercondylar notch
5.0 Upper third (permanent) premolar
5.1 large parastyle
5.2 hypocone absent
5.3 undivided parametacone
5.4 buccal cingulum present
5.5 high clearly expressed mesostyle
5.6 wide, deep posterior fossa, distinctively worn
6.0 Upper molars
6.1 weak parastyle, strong postparaconal crest
6.2 strong, short, rounded lingual cingulum
6.3 small protostyle M^2
6.4 M^5 in line with M^4 lingually
6.5 P^3 widely contacts M^2 interproximally
6.6 metalophs sharply reduced M^{4-5}
6.7 metastyles low on PMC, strong on M^4
6.8 labial cingulae short, thick, rising confined to MV
7.0 Dentary
7.1 body deep, tapers anteriorly
7.2 diastemal crests, long high, anteriorly expanded
7.3 near horizontal symphysis, terminates behind M_2
7.4 short, shallow digastric fossa
7.5 genial pits in ventral border of symphysis
8.0 Lower incisors
8.1 wide, thick crowns
8.2 nearly horizontal implantation
8.3 enamel on all surfaces
8.4 thick cementum base raised above enamel
9.0 Lower third premolar
9.1 small relative to molars
9.2 narrow, oval crown
9.3 weak buccal cingulum present
9.4 large central cuspid, short posterior moiety
10.0 Lower molars
10.1 paralophid crest weak, protolophid face steep
10.2 protolophids $M_{2,3}$ high relative to hypolophids
10.3 midvalleys V-shaped
10.4 lingual offset of P_3-M_2
10.5 weak, short precingulid
10.6 reduced size of M_5

Upper cheek dentition: The P^3 is a short, broadly trilobate tooth composed of a large, high, transversely oval-sectioned parastyle with a slight buccal offset of the apex, a high, pyramidal, undivided parametacone and a robust, conical but slightly lower protocone (Figs 7-9; Table 4). The hypocone is absent. The apex of the parastyle is set closer to the parametacone than in *Plaisiodon*, but closely resembles it proportionally. The buccal groove separating the parastyle from the parametacone is deeper, longer and more cleft-like than in any other zygomaturine genus. The anterolingual basin is deeper, more confined and forms a more definitive horizontal shelf than in *Neohelos* or *Plaisiodon*. The anterolingual cingulum is short but distinct, commencing from the mid-lingual base of the parastyle to ascend the anterolingual aspect of the protocone, forming near its base, a minute protostyle. A distinct secondary basin, slightly elevated above the parastylar basin, lies immediately anterior to the base of the protocone. This preprotoconal basin is incipient in *Neohelos*, distinct but small in *Kolopsis* and variably expressed in *Plaisiodon*, in which its presence is associated with a reduction of the parastylar basin. A protostyle is present in some *Neohelos* and *Kolopsis* specimens, but appears to be absent in *Plaisiodon*. The protocone is large, though slightly smaller than the parametacone and higher, relative to the parametacone than in *Neohelos*, *Plaisiodon* and *Kolopsis*.

In section, the protocone of *Alkwertatherium* approximates a rounded trapezoidal shape compared to the distinctly rounded section of the cusp in *Plaisiodon* and *Pyramios*. A short, thick postprotocrista ascends the cusp near vertically, becoming indistinct immediately short of the lingual portion of the postcingulum. The postcingulum is well-developed lingually, becoming indistinct interproximally and distobuccally. The posterior surfaces of the parametacone and protocone are steep and delineate the sides of a deep, oval distal basin, exaggerated to some extent perhaps, by wear. Although there is ample room on the posterolingual shelf for a hypocone, not so much as a thickening of the cingulum can be found to betray a phenotypic expression of the structure.

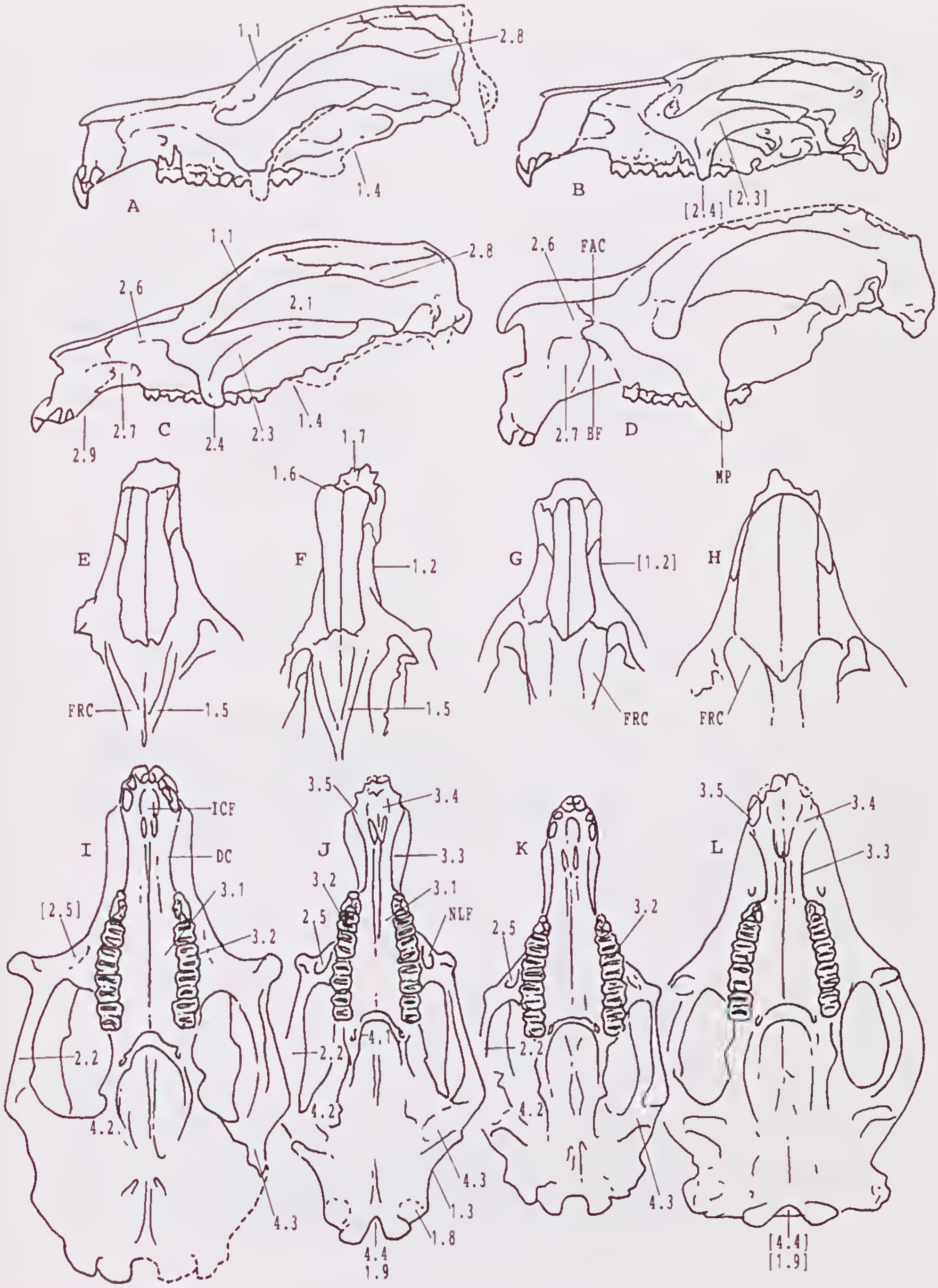

Fig. 6. Character distribution comparison of the cranium of *Alkwertatherium webbi* with crania of the larger mid- to late Miocene diprotodontid genera. **A**, *Plaisiodon centralis*, (holotype CPC 6784, restored from cast SGM 884); **B**, *Neohelos tirarensis* (NTM P8695-38); **C**, *Alkwertatherium webbi*, (SGM 888) restored; **D**, *Pyramios alcootense* (holotype cranium CPC 6749, partially restored) (after Woodburne 1967); **E**, dorsal aspect of snout of *P. centralis* (from cast SGM 884); **F**, *A. webbi*; **G**, *N. tirarensis*; **H**, *P. alcootense* (after Woodburne 1967); **I**, ventral aspect of *P. centralis* SGM 871 (restored); **J**, *A. webbi* (restored); **K**, *N. tirarensis*; **L**, *P. alcootense*, (restored) (after Woodburne 1967). Numerical references to characters are given in Table 4. Corresponding numbers indicate a strong similarity; brackets indicate a variable condition or less distinct, though similar features. Abbreviations: **FRC**, frontal crest; **FAC**, facial crest; **BF**, buccinator fossa; **MP**, masseteric process; **ICF**, Interincisive fossa; **DC**, diastemal constriction; **NLF**, nasolabial fossa.

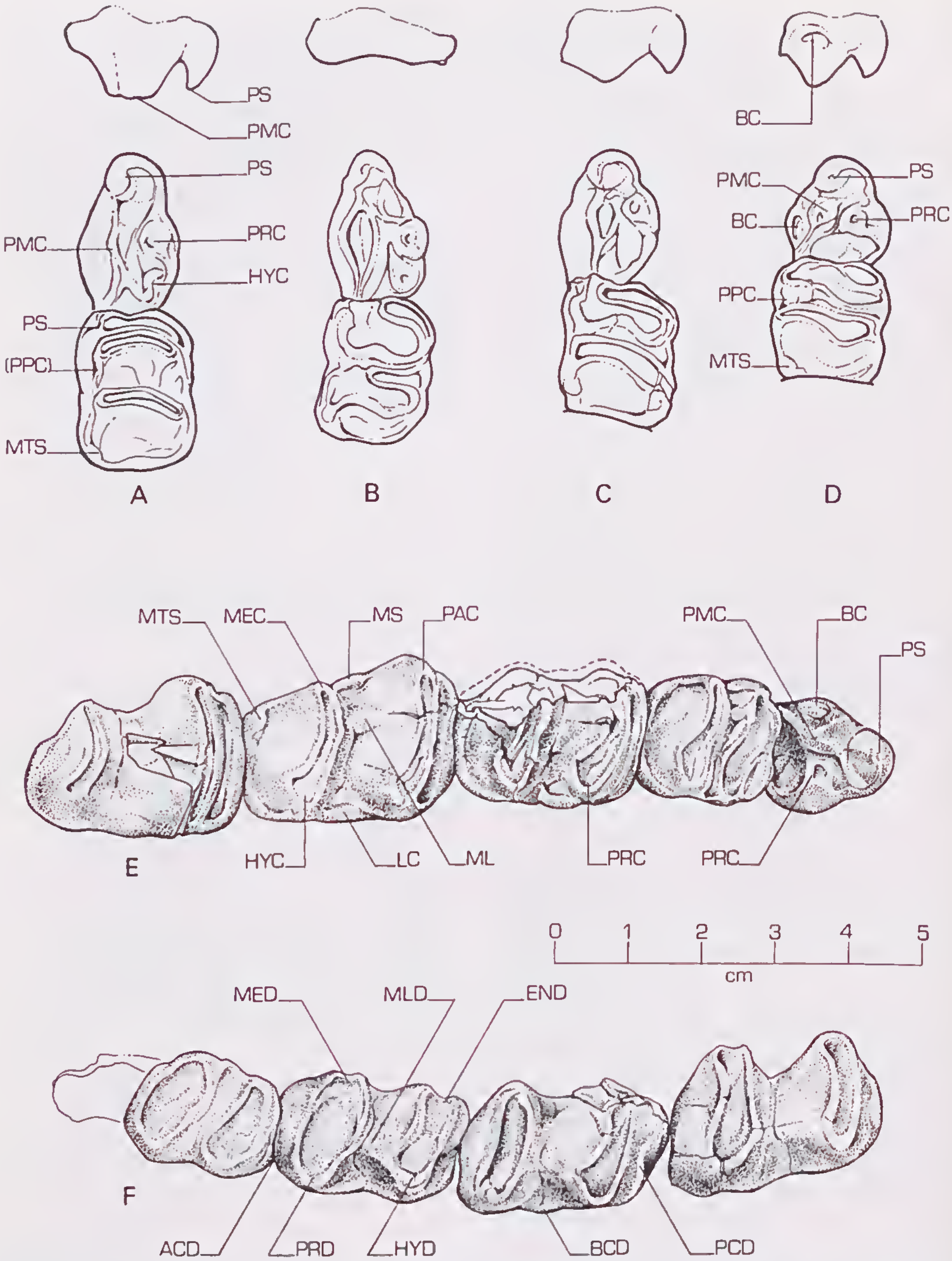

Fig. 7. Upper cheek dentition of *Alkwertatherium webbi*. (**A-C**) comparison of P^3-M^2 of *Plaisiodon centralis* with (**D**) *Alkwertatherium webbi*. **A-C**, range of morphological variation in cusp morphology of *Plaisiodon centralis*; **C**, "hypoconeless variant" which has a thickening in the lingual cingulum; in **B**, the parastyle is exceptionally worn. Note the narrow labiad interproximal contact of the P^3 with M^2 in *Plaisiodon*; **E**, upper cheek tooth row of *Alkwertatherium webbi*; **F**, lower cheek tooth row of *Alkwertatherium webbi*. Abbreviations: **PS**, parastyle; **PMC**, parametacone; **PRC**, protocone; **HYC**, hypocone; **PPC**, postparaconal crest; **MTS**, metastyle; **BC**, buccal cingulum; **ML**, midlink; **PAC**, paracone; **MS**, mesostyle; **MEC**, metacone; **MED**, metaconid; **END**, entoconid; **ACD**, anterior cingulid; **PRD**, protoconid; **HYD**, hypoconid; **BCD**, buccal cingulid; **PCD**, postcingulid; **MLD**, metalophid or cristid obliqua.

Apparently "hypoconeless" variants of *Neohelos* usually show a thickening of the cingulum in the position of the hypocone. The posterior portion of the tooth is more similar to that of *Pyramios*, both structurally and thegotically, except that the posterolingual portion of the postcingulum is more generous in *Alkwertatherium*. The low, interproximally indistinct postcingulum commences on the distobuccal corner of the parametacone after which it ascends the posterolabial margin of the cusp in the form of a steep, thick, slightly irregular postparametacrista, narrowing gradually as it approaches the apex of the cusp. The parametacone is steep and triangular in section with the anterior face presenting a transversely flattened, apically tapering surface. A distinct cuspule is present immediately lateral to and below the apex of the parametacone. This mesostyle (possibly homologous with stylar cusp C of primitive vombatiform molars) is continuous with the posterobuccal cingulum, which in *Alkwertatherium* defines a distinct, oval fossette on the distobuccal flank of the parametacone.

The P^3 of SGM 872, *Pyramios alcootense*, is similar to *Alkwertatherium* in the shape of the parametacone and the degree of development of the postparametacrista. A posterobuccal cingulum is present but does not establish a fossette. The mesostyle is larger but less distinctly defined. There is a faint postparastylar sulcus separating a small parastyle from the parametacone and defining the anterior extent of the mesostyle. None of the *Pyramios* third premolars show a tendency to develop more than an incipient parastyle, although the anterior crown base is more generous than in other nototheriines, being more comparable to that of zygomaturines, and a faint buccal crease, delineating the base of the parastyle, is present on some specimens. The large size of the P^3 and the incipient parastyle development gives the impression that *Pyramios* is structurally intermediate to nototheriines (Diprotodontinae) and zygomaturines.

The upper molars of *Alkwertatherium*, in comparison with similar-sized CPC 6748, *Plaisiodon centralis*, are smaller relative to the splanchnocranium, particularly M^{4-5}, which do not abruptly widen behind the third molar as in *P. centralis*. This marked transition in the molar gradient in *P. centralis* is a distinctive and consistent feature of the species, and indeed among zygomaturines in general. There are two other consistent differences in the morphology of the arcade: in *Alkwertatherium* the interproximal contact between the P^3 and M^2 is wide and centered, and the M^5 is aligned with the M^4 on the lingual side. In *Plaisiodon centralis* the P^3 is offset buccally leaving a large V-shaped gap between the teeth on the lingual side, and the M^5 is offset lingually creating a step-like contour of the occlusal profile on the lingual side. The primary differences in molar morphology between *Alkwertatherium* and *P. centralis* are in the degree of development in the buccal and lingual cingulae and crests related to the posterior margins of the lophs.

The second molar in *Alkwertatherium* is distinctive in having a wider mid-valley buccally and in possessing a well-developed buccal cingulum, continuing anteriorly into a short postparaconal crest. The parastyle is poorly developed on all molars. The molar crown morphology is otherwise very similar in the two species and the discrimination of isolated molars is complicated by a high degree of morphological variability.

The M^2 of *Alkwertatherium* has a weakly developed parastyle, but a distinct, short, postparastylar crest. A short postparaconal crest ascends the base of the paracone and is continuous with a thick buccal cingulum which spans the mouth of the interloph valley to the base of the hypocone, where it is transected by a faint sulcus. The cingulum bulges slightly as a presumptive mesostyle. The protoloph is slightly wider and more massive than the metaloph. A low, short, midlink is present and a second, faint crest transects the interloph valley just lingual to the longitudinal midline of the crown. The postcingulum is wide and rounded. Buccally it ascends the metacone as a distinct postmetacrista, at the base of which is developed a low, indistinct metastyle. Lingually, the postcingulum terminates near the base of the hypocone and is separated by the lingual side of the metaloph from a short lingual cingulum that flares out around the mouth of the interloph sulcus. At its anterior extreme, a small protostyle is present. The anterior cingulum is wide lingually and slightly thickened on the midline.

The M^3 is larger than the M^2 with a distinctly wider lingual interloph sulcus and correspond-

Fig. 8. Scatter diagram of the dimensions of upper cheek teeth comparing *Alkwertatherium* (triangles) with *Plaisiodon* (dots) and *Pyramios* (squares); data from Woodburne (1967a) with the addition of new specimens listed under Comparative Material of *A. webbi*. Note the relatively clear separation of genera with the premolar compared to the large degree of overlap with the molar dimensions. *Alkwertatherium webbi* aligns with *Pyramios alcootense*. Scale is in millimetres, X axis = width, Y axis = length; regressions were not calculated due to to small sample size.

ingly longer lingual cingulum. The protostyle is reduced to a low bulge. The "midlink" (which does not appear to be homologous with a crista obliqua), is a teardrop-shaped enamel boss developed on the base of the paraconal side of the protoloph. The interloph valley is sinuous, deep and narrow. Both moieties are approximately equal-sized. The postmetacrista is indistinct. The postcingulum is reduced lingually but remains wide and low on the posterobuccal corner of the metaloph, where a low metastyle is present.

The M^4 is larger than M^3 and is distinguished by its narrower metaloph, wide protoloph and buccally expanded paracone, wider midvalley, less well-developed postcingulum and less distinct though broader "midlink". The M^5 closely resembles M^4 in size and shape, but the metaloph is relatively narrower, the postcingulum is confined to the posterobuccal side of the crown, the midlink is reduced to a faint swelling and the buccal cingulum is absent.

Although the molars are indeed distinctive, there are no individual characters of the crown morphology that can invariably separate them from *Plaisiodon centralis* or from *Pyramios alcootense*. Except for their smaller size, slightly greater apparent obliquity of the lophs of M^{2-3} and the difference in the molar gradient, the degree of variability in *Plaisiodon* crown morphology, and indeed, even the differences between the right and left sides of the *Alkwertatherium* cheek dentition, render the distinction of isolated teeth somewhat dubious, given that the size range of *Alkwertatherium* is unknown. Worn molars, particularly M^2, have a distinctive thegotic character which will be discussed in conjunction with the lowers. The molar gradient, dimensions, and the low disposition of the metasyle on M^2 of *Alkwertatherium* more closely resembles *Pyramios*, but the proportional widths of protoloph to metaloph for each molar, the occlusal contours, particularly M^{4-5}, with a marked reduction of the width of the metaloph, are more similar to *Plaisiodon*.

Dentary: The associated dentary of *Alkwertatherium* superficially resembles that of *Palorchestes* in having an extremely long, kangaroo-like, horizontally disposed symphysis, containing broad, spatulate, procumbent lower incisors (Figs 10-11). The molars are typical of diprotodontids and most closely resemble those of the nototheriine, *Pyramios alcootense*. Although the dentary was found in association with the cranium of *Alkwertatherium*, which was isolated from other fossil concentrations, direct association of fossils in the Alcoota assemblage is no guarantee that the remains represent a single individual.

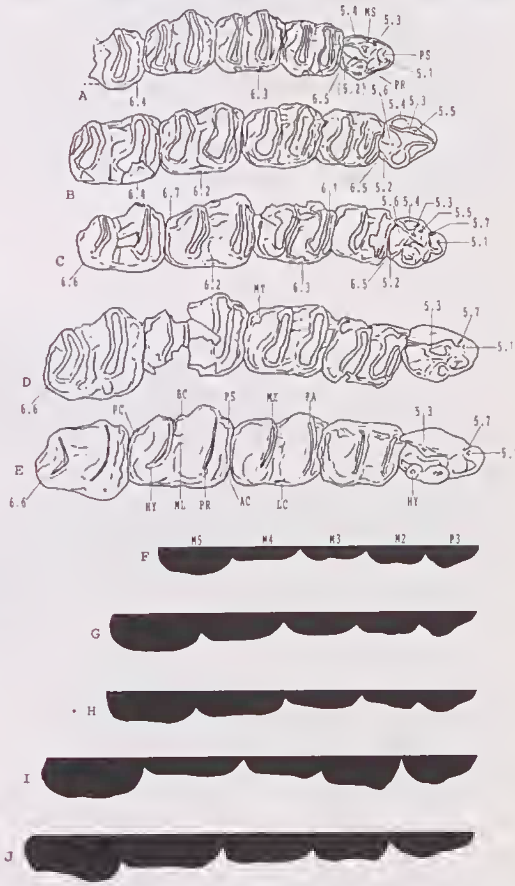

Fig. 9. Comparisons of the upper cheek dentitions of larger mid- to late Miocene diprotodontid genera with *Alkwerthatherium webbi*. **A**, *Neohelos tirarensis* (NTM P8690) "hypoconeless variant"; **B**, *Pyramios alcootense* (SGM [R]872); **C**, *Alkwertatherium webbi* (SGM [R]888); **D**, *Plaisiodon centralis* (SGM [R]887); **E**, *Plaisiodon centralis* (SGM 885); **F**, lingual occlusal profile of *Neohelos tirarenesis* (NTM P8690) compared with **G**, *Pyramios alcootense* (SGM [R]872); **H**, *Alkwertatherium webbi* (SGM 888); **I**, *Plaisiodon centralis* (SGM [R]887); **J**, *Plaisodon centralis* (SGM 885). Abbreviations: **MS**, mesostyle; **PS**, parastyle; **PR**, protocone; **MT**, metastyle; **PC**; postcingulum; **HY**, hypocone; **BC**, buccal cingulum; **ML**, midlink; **AC**, anterior cingulum; **LC**, lingual cingulum; **ME**, metacone; **PA**, paracone. Numerical references to the characters are listed in Table 4. The lingual profiles of the molars show the step-like offset of M^5 in *Plaisiodon*, in comparison to the other genera. There is a tendency towards this condition in some *Neohelos* and some *Pyramios* (F, G); but the trait is apparently not present in *Alkwertatherium webbi*.

However, there are occasionally isolated pockets in which partially articulated material is recovered. *Alkwertatherium* occurred in one of these situations. The dentary lay slightly above and at the posterior end of the cranium with the dentitions of both facing upwards. As the excavation around the dentary progressed, the cranial base of SGM P888 was partially exposed immediately beneath the posterior end of the inferior border of the dentary, the anterior ends of the jaws and cranium pointing away from one another, as though the dentary had been dislodged backward from the skull.

To the extent that the somewhat distorted lower tooth rows can be physically occluded with the uppers, they match closely in terms of occlusal surface angles of the similarly worn lophs and lophids, the distance between them, and in terms of the individual variations of each tooth in the degree of wear, pattern of attrition and thegotic correspondence.

The dimensions of the individual molar teeth are also within the expected tolerances for the same individual which ranges normally between 0.85 and 1.0. The length of the right uppers from front to back are: 23.3, 27.1. 28.7,

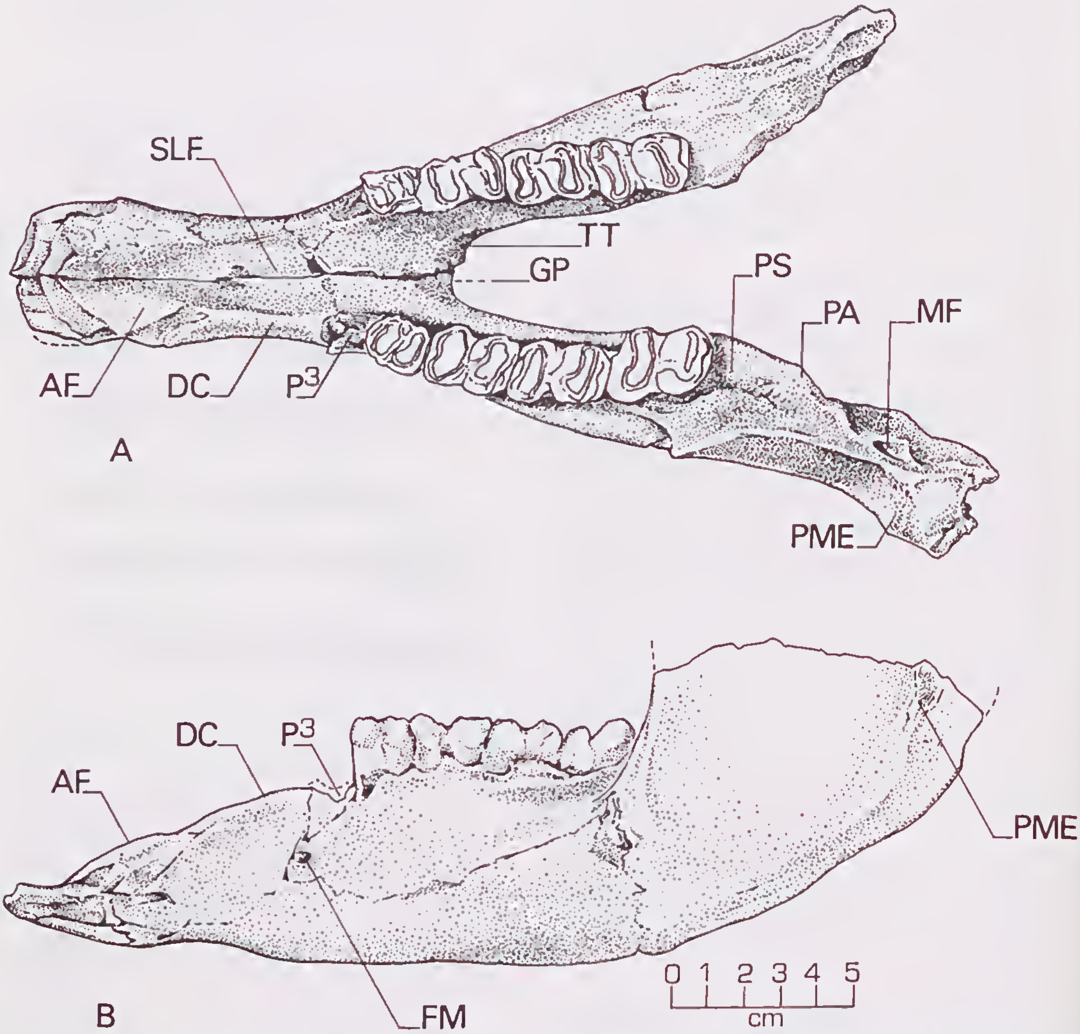

Fig. 10. Dentary of *Alkwertatherium webbi* gen. et sp. nov. (SGM 883, paratype). A, occlusal aspect; B, lateral aspect. Note the extreme procumbency of the lower incisors, anteriorly tapering horizontal ramus, high long diastemal crests and their bony expansions, long deep, sublingual fossa and short, weak transverse torus penetrated by genial pits. The symphysis, which is unfused, extends to the posterior moiety of M_2. Abbreviations: **SLF**, sublingual fossa; **DC**, diastemal crest; **AF**, anteriorly flattened surfaces of diastemal crests; **GP**, genial pit; **TT**, transverse torus; **PS**, postalveolar shelf; **PA**, postalveolar process; **MF**, mandibular foramen; **PME**, posterior masseteric eminence; **FM**, mental foramen.

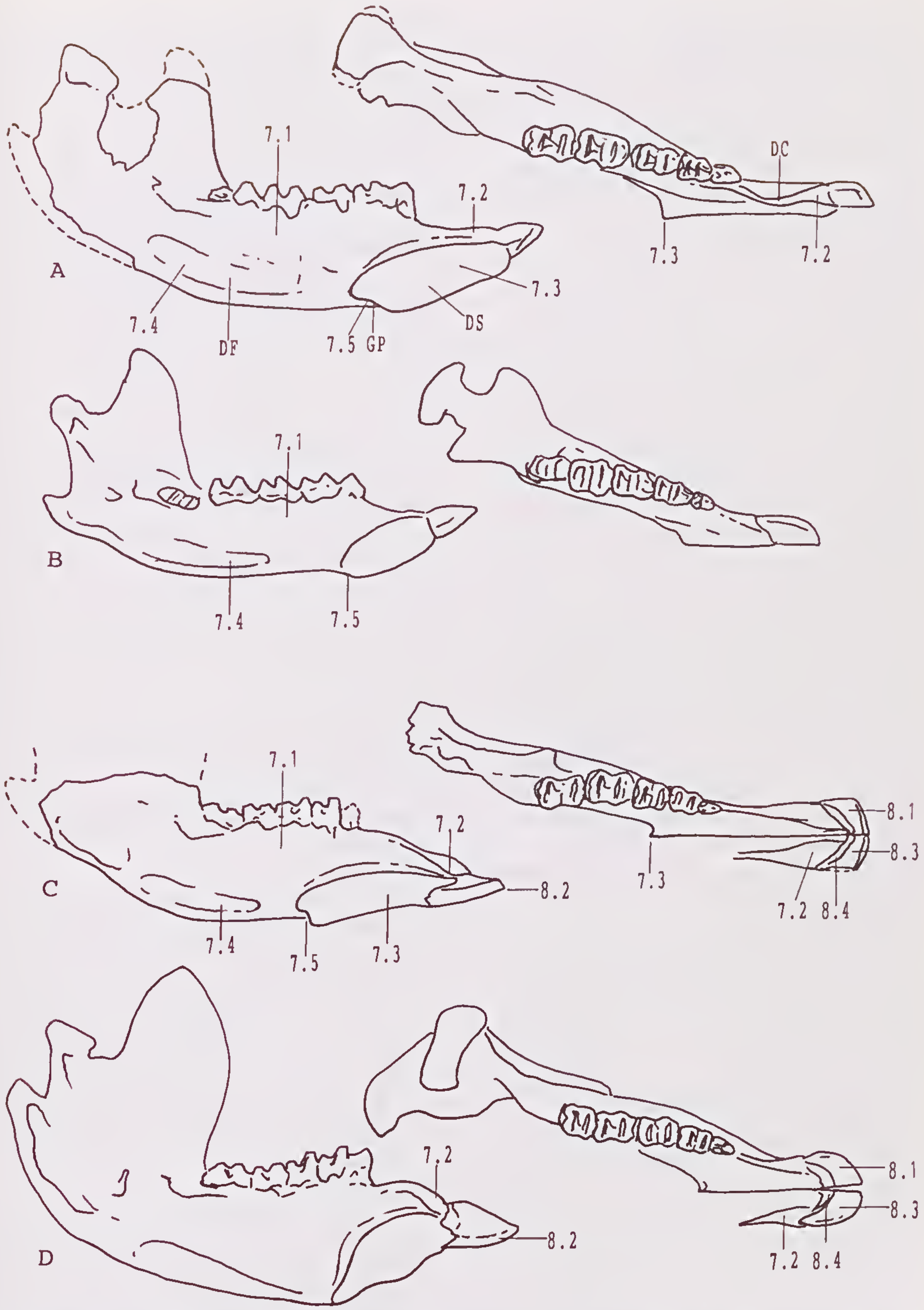

Fig. 11. Comparison of the dentaries of larger mid- to late Miocene diprotodontids with *Alkwertatherium webbi*. **A**, *Plaisiodon centralis* (SGM 881); **B**, medial aspect (left) and occlusal aspect (right) of *Neohelos tirarensis* (CPC 22530); **C**, *Alkwertatherium webbi* (paratype SGM 883); **D**, *Pyramios alcootense*, (SGM 891). Numerical character definitions are given in Table 4. Abbreviations: **DC**, diastemal crest; **DF**, digastric fossa; **DS**, dentary symphysis; **GP**, genial pit.

27.7. The right lowers are 18.3, 22.1, 25.8, 27.4; resulting in a proportional congruence of 0.87. The distance between the lophs and lophids for each occluding pair are as closely matched as can be determined by simple measurements. The congruence of the lower incisors with the upper incisor sockets appears to be close. Presumably the low angulation and buccal offset of the empty upper incisor sockets is disposed to the accomodation of the broad, procumbent lower incisors.

The dentary of *Alkwertatherium* differs from that of the nototheriine *Pyramios alcootense* in having a nearly straight inferior border of the horizontal ramus, an anteriorly tapering and more slender as opposed to a more massive, anteriorly deep, posteriorly tapering body; much shorter and vertically narrower, more horizontal diastemal portion, and a much longer and more horizontally disposed symphysis that extends to behind M_2 as opposed to behind the P_3. In *Pyramios alcootense*, the dorsal contour of the symphysis (sublingual sulcus) is nearly vertical in SGM P891. Ventrally, in *Pyramios*, a distinct mental eminence is developed immediately below the incisor alveoli. This is also evident in the paratype UCMP 69784. The dentary is similar to, though much smaller than any mature specimen of *Plaisiodon centralis*, differing principally from that genus in the more procumbent incisor alveolus and relatively longer diastemal portion of the jaw. The symphysial outline is more similar to *Plaisiodon* than it is to *Pyramios*.

The horizontal ramus is relatively deeper in proportion to length than in *Plaisiodon*, but it is also proportionally less thick in section below the molar alveoli. The diastemal crests of *Alkwertatherium* are much thicker, higher and less sinuous than in *P. centralis*. Anteriorly, the diastemal crests become laterally expanded, flat surfaces paralleling the subhorizontally implanted incisor crown bases. The diastemal crests of *Pyramios* are similar, though more arched dorsally, much shorter and less expanded anteriorly than in *Alkwertatherium*. Internally, the digastric sulcus is slightly deeper than in either *Pyramios* or *Plaisiodon* and extends further anteriorly than in the latter but not as far anteriorly as in the former genus. The position of the genial pits is also intermediate between *Pyramios*, in which they are on the posterior surface of the symphysis and *Plaisiodon*, in which they are situated on the ventral surface. In *Alkwertatherium*, the genial pits penetrate the ventral surface of the symphysis, but extend onto the posterior surface as well.

Lower dentition: The lower incisors are extremely wide, thick, spatulate horizontally implanted teeth that repose with the lateral margin of the crown at about ten degrees from horizontal (Figs 5, 10-11; Table 1). *Plaisiodon centralis* incisors are only moderately spatulate, with the crowns oriented about 55 degrees from horizontal in frontal aspect, and lying at about 35 degrees from horizontal in lateral aspect, being considerably less procumbent than in *Alkwertatherium*. The lower incisor implantation of *Pyramios* is nearly horizontal, as in *Alkwertatherium*, but the symphysial angle is substantially more steeply inclined and extends far deeper below the alveoli. The frontal implantation angle of the incisor crowns in *Pyramios* is acute. The internal angle of the paired incisors of *Pyramios* is V-shaped at between 80 and 85 degrees. In *Alkwertatherium* the internal angle (dorsal surfaces) of the paired incisors presents an obtuse surface of approximately 120 degrees.

The enamel extends entirely around the crown of the lower incisors of *Alkwertatherium*, as in *Pyramios*, in contrast to its being confined to a narrow strips on either side of the dorsal surface of the crown as in the zygomaturine *Plaisiodon centralis*. The severely worn tips of the crowns of *Alkwertatherium* lower incisors precludes a description of their original shape, but there can be little doubt that they were very similar to those of *Pyramios alcootense*. The transverse width of the crown is at least 28 mm and about 10 mm thick medially, near the base of the crown. The crowns are thicker medially, tapering towards the external margins. The cementum is raised above the enamel on the dorsal surfaces forming a continuation with the broad, bony diastemal platform.

The P_3 of the paratype dentary SGM P883 was broken off, then placed in a small box which was subsequently mislaid during transportation of the specimens from the field. It was exceptionally small relative to the molars. Fortunately it is well preserved on SGM P892, a right dentary fragment of *Alkwertatherium* (Figs 12-13). The P_3 has a small, oval crown

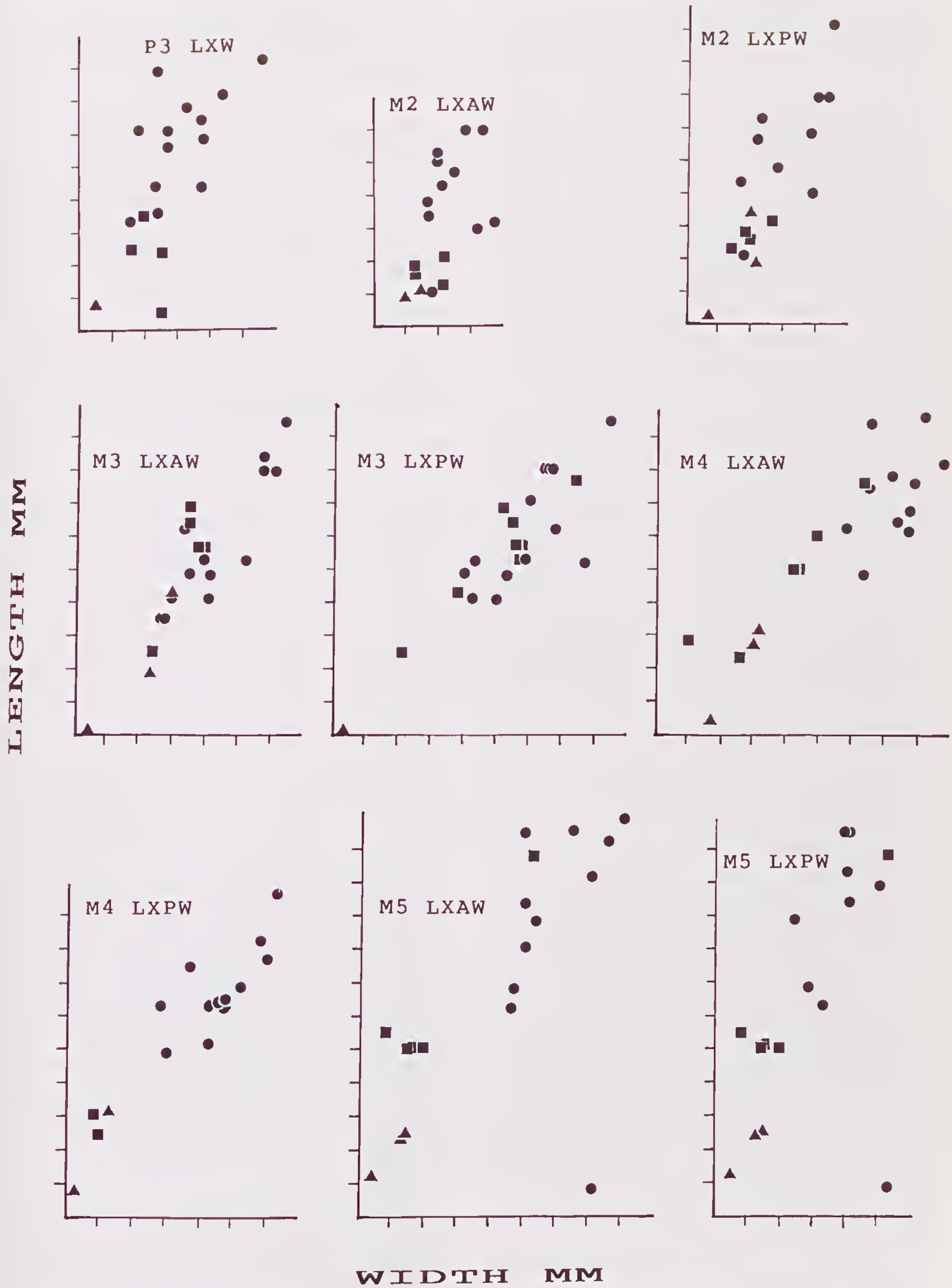

Fig. 12. Scatter diagram of the dimensions of lower cheek teeth of *Alkwertatherium webbi* (triangles), *Plaisiodon centralis* (dots) and *Pyramios alcootense* (squares). As with the upper dentitions, *Alkwertatherium* is more closely aligned with *Pyramios alcootense*. Data from Woodburne (1967a) and new specimens given in materials list. Regressions were not calculated due to small sample of *Alkwertatherium*.

composed of a large central cuspid and a median cristid which extends back to the interproximal contact with M_2 and is conjoined by a weak buccal and a more distinct lingual cingulum. The buccal cingulum trends obliquely towards the anterior edge of the posterior root, then faintly ascends the flank of the central cuspid to define a shallow, U-shaped fossa. The posterolingual cingulum surrounds a kidney-shaped basin. Structurally the P_3 crown is more similar to that of a zygomaturine (e.g. *Plaisiodon centralis*) and differs from that of *Pyramios* in being smaller, relatively narrower, shorter posterior to the central cuspid, in possessing a buccal cingulum and in lacking a clearly defined transverse crest from the central cuspid.

The lower molars are similar to those of *Pyramios alcootense* (Fig. 13). *Alkwertatherium* has a distinct but low paralophid crest and a steep, high protolophid on the M_2. This high protolophid relates thegotically to the correspondingly low protoloph of the upper and the deeply worn posterior fossa of the P_3 and anterior cingulum of M_2. With the exception of M_2, the protolophids are wider than the hypolophids. The M_2 is relatively small, and the gradient is that of a gradual front to back increase in size. The lophids of $M_{2\text{-}3}$ are more obliquely oriented than the other molars. The protolophid of M_3 is also much higher than the hypolophid. The interlophid valleys of the first two molars are more sinuous and steeply V-shaped than in the last two. A short, low precingulum is present on the lingual side of the anterior base of the protolophid. Its expression diminishes gradually from front to back. A low cristid obliqua is present on all molars, extending from the hypoconid down the anterior face of the hypolophid to the base of the posterior face of the protolophid in the approximate longitudinal midline of the tooth. Weak cingulae occur in the buccal and lingual mouths of the interloph sulcus. The postcingulum is thick, relatively deep and rounded. It is elevated slightly near the longitudinal midline of the tooth, commencing on the labial side proximally and swinging gradually toward the lingual side distally.

Etymology. The species designation "*webbi*" is made in gratitude to Thomas and Wendy Webb of Alcoota Station, Northern Territory, for their valued support in palaeontological research at Alcoota.

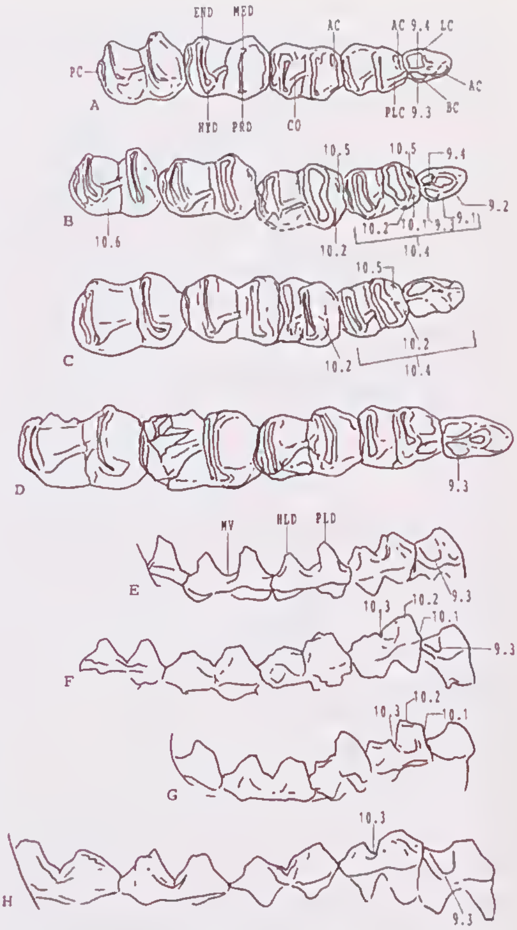

Fig. 13. Comparison of the lower cheek dentitions of the larger mid- to late Miocene diprotodontid genera with *Alkwertatherium webbi*. **A**, *Kolopsis torus* (SGM 893); **B**, *Alkwertatherium webbi* (paratype SGM 892); **C**, *Pyramios alcootense* (SGM 891); **D**, *Plaisiodon centralis* (SGM 881); **E**, labial aspect of dentition of *Kolopsis torus* (SGM 893); **F**, *Alkwertatherium webbi* (SGM 892); **G**, *Pyramios alcootense* (SGM 891); **H**, *Plaisiodon centralis* (SGM 881). Numerical references to character definitions are given in Table 4. Abbreviations: **END**, entoconid; **MED**, metaconid; **HYD**, hypoconid; **PRD**, protoconid; **CO**, cristid obliqua; **PLC**, paralophid crest; **BC**; posterobuccal cingulid; **AC**, anterobuccal cingulid; **MV**, midvalley (U-shaped in *Kolopsis torus*, as considered typical of zygomaturines); *HLD*, hypolophid; *PLD*, protolophid.

Analysis of characters. The morphological description of *Alkwertatherium webbi* broadly samples comparable morphological features, of which only a few are specifically useful in diprotodontid systematics (Tables 3, 5; Figs 6, 8, 11, 13). Many important features (suture configurations, upper incisor morphology etc.) could not be considered due to the poor state of preservation of the specimen. Though incomplete, this constellation of characters is adequate to formulate an hypothesis of the approximate systematic position of *Alkwertatherium*.

Based primarily upon the work of Stirton *et al.* (1967) and subsequently Archer and Bartholomai (1978), Aplin and Archer (1987), the Diprotodontidae can be divided into two subfamilies, the Zygomaturinae and the Nototheriinae or Diprotodontinae. Recent revisions have sunk the Nototheriinae. Consensus purports that the two groups of diprotodontids, the Zygomaturinae, with a well-developed parastyle on the upper third premolar and the Diprotodontinae which either lack or have small parastyles, are monophyletic. It is assumed that the large zygomaturine parastyle is a synapomorphic character. However, in the case of the Diprotodontinae, the absence or small size of the parastyle is a symplesiomorphic state.

Diprotodontines are also descriminated from zygomaturines on the basis of tighter, more V-shaped interlophid valleys; "cleaner", less complex internal loph faces; high, steep protolophid of the M_2; suppression of the paralophid crest; weak anterior cingulid; strong postparaconal crest on the upper molars; reduced size of the upper and lower premolars relative to the size of the molars, and a greater obliquity of the molar lophs and lophids. In derived forms (*Diprotodon*), the lophs (-ids) of the molars are hypsodont.

This character complex may succeed in distinguishing the later Tertiary Diprotodontinae from the Zygomaturinae, but *Pyramios alcootense* variably expresses zygomaturine-like midlinks, complex interloph shapes and cingulum configurations, as well as possessing an upper third premolar that is consistently as large relative to M^2, as in for example, the zygomaturine, *Neohelos*.

Pyramios alcootense aligns with diprotodontines in having a steep, high protolophid on the M_2, a suppressed, practically nonexistent, paralophid crest; in the molar gradient of the uppers, in which there is a simple front-to-back enlargement and in which the metaloph is not as reduced relative to the protoloph as in zygomaturines, and of course, the upper third premolar, which lacks a well-developed parastyle. In cranial characters, *Pyramios* resembles *Euryzygoma* in its diastemal constriction, deep, broad cranium and short, posteriorly divergent molar arcades. However, the I^3's in *Euryzygoma* and *Diprotodon* are in line with the I^2's and the zygomatic processes are flat-sided.

The lower incisor morphology, relatively wide though V- shaped interlophid valleys, weak cristid obliquae and comparatively low

Table 5. Distribution of characters in representatives of four diprotodontoid families. 1, wynyardiid (*Muramura williamsi*); 2,"palorchestid" (*Ngapakaldia*) and 3, palorchestine (*Propalorchestes*) examples represent the outgroup; 4, diprotodontine (*Pyramios alcootense*); 5, zygomaturine (*Alkwertatherium webbi*); 6, zygomaturine (*Neohelos tirarensis*); 7, zygomaturine (*Plaisiodon centralis*); 8, zygomaturine (*Kalopsis torus*). Symbols: o=absent; +=present; ±=more or less present; -=not observed; ?=unsure of homology; AP=apomorph, PL=plesiomorphy.

	1	2	3	4	5	6	7	8	CHARACTER DISTRIBUTION AND STATE
1.1	o	o	o	o	+	o	+	o	long, high steep frontal (AP)
1.2	o	o	o	o	+	o	o	o	constricted preorbitally (AP)
1.3	+	o	o	o	+	+	+	o	postsquamosal constriction (PL)
1.4	o	±	o	o	+	o	+	o	upward BC flexion (AP)
1.5	+	+	o	o	+	o	+	o	thin frontal crests (PL)
1.6	o	o	o	o	+	+	+	+	nasals expand anteriorly (AP)
1.7	o	o	o	o	+	+	+	o	trapezoid narial aperture (AP)
1.8	+	o	o	o	+	+	o	o	low, narrow occiput (PL)
1.9	o	+	+	+	+	+	+	+	wide, oval foramen magnum (PL)
2.1	o	o	+	+	+	o	o	o	long squamosal process (AP)
2.2	o	+	+	o	+	+	+	+	flattend zygomatic arch (PL)
2.3	o	o	o	o	+	o	o	o	zygomatic deeper anteriorly (AP)
2.4	+	+	o	o	+	+	o	+	short masseteric processes (PL)
2.5	+	+	o	o	+	+	+	+	deep nasolabial fossa (PL)
2.6	o	o	o	+	+	o	o	o	distinct facial crest (AP)
2.7	o	o	o	+	+	o	o	o	distinct buccinator fossa (AP)
2.8	+	+	+	o	+	+	+	o	long squamosal sulcus (PL)
2.9	o	+	?	+	+	o	o	o	shallow diastemal profile (AP)
3.1	o	o	+	o	+	o	+	o	long, narrow palate (AP)
3.2	+	+	+	o	±	+	+	+	arcades parallel, straight (PL)
3.3	o	o	+	+	+	o	+	o	constricted diastema (AP)
3.4	o	o	+	+	+	o	o	o	flared premaxillary palate (AP)
3.5	o	o	+	+	+	o	o	o	I^3 lateral to I^2 (AP)
4.1	+	o	o	o	+	o	o	o	narrow, shallow IP fossa (PL)
4.2	-	+	+	+	+	+	+	+	small pterygoid fossae (PL)
4.3	o	o	o	o	+	+	+	+	oblique glenoid fossae (AP)
4.4	o	o	±	o	+	o	o	o	deep, V-shaped condylar notch AP)
5.1	?	o	o	o	+	+	+	+	large parastyle on P^3 (AP)
5.2	+	+	+	+	+	o	o	o	hypocone absent (PL)
5.3	+	+	+	+	+	+	+	o	undivided parametacone (PL)
5.4	o	o	o	+	+	+	o	+	buccal cingulum present (PL)
5.5	?	±	+	+	+	o	o	o	high, large mesostyle (PL)
5.6	o	o	+	+	+	o	o	o	functional posterior basin (AP)
6.1	+	+	+	+	+	o	±	o	weak parastyle, strong PPC (PL)
6.2	o	o	o	±	+	o	±	o	thick, short, rounded LC (AP)
6.3	o	o	o	o	+	o	±	o	protostyle on M^2 (AP)
6.4	+	+	+	±	+	o	o	o	M_4-M_5 in line lingually (PL)
6.5	+	+	+	+	+	o	o	o	P^3 widely contacts M^2 (PL)
6.6	o	o	o	o	±	+	+	+	Metaloph reduction M^{4-5} (AP)
6.7	o	o	o	o	+	o	o	o	large metastyle low on M_4 (AP)
6.8	o	o	o	+	+	o	+	o	short, thick buccal cingulum (AP)
7.1	+	+	+	o	+	+	+	+	deep ramus tapers anteriorly (PL)
7.2	o	o	+	+	+	o	+	o	strong diastemal crests (AP)
7.3	o	o	+	o	+	o	±	o	long, horizontal symphysis (PL)
7.4	o	o	+	+	+	o	o	o	short, weak digastric fossa (AP)
7.5	+	+	+	+	±	+	+	+	genial pits ventral surface (PL)
8.1	o	o	+	+	+	o	o	o	spatulate I_1 crown (AP)
8.2	o	o	+	+	+	o	o	o	horizontally implanted I_1 (AP)
8.3	o	o	+	+	+	o	o	o	enamel all sufaces I_1 crown (AP)
8.4	o	o	o	+	+	o	o	o	cementum raised above enamel (AP)
9.1	o	+	o	o	+	o	o	o	P_3 small relative to molars (PL)
9.2	o	+	o	o	+	o	o	o	narrow, oval crown of P_3 (PL)
9.3	o	o	o	o	+	+	+	+	buccal cingulum present on P_3 (AP)
9.4	o	o	+	o	+	+	o	+	short posterior moiety P_3 (PL)
10.1	o	o	+	+	+	o	o	o	steep protolophid, weak crest (AP)
10.2	o	o	+	+	+	o	o	o	protolophids higher (AP)
10.3	+	+	+	+	+	o	o	o	V-shaped mid valleys (PL)
10.4	o	o	o	+	+	o	o	o	lingual offset P_3 (AP)
10.5	o	o	+	+	+	o	o	o	weak, short precingulid (AP)
10.6	o	o	o	o	±	+	+	+	reduced M_5 (AP)

lophs and lophids of *Pyramios* are not suggestive of a close relationship to *Euryzygoma* or any other later Tertiary notothere (Woodburne 1967a, 1967b).

Having noted these discrepencies in combination with the geologically late occurrence of *Pyramios*, Woodburne (1967a, 1967b) characterized *Pyramios* as a primitive nototherere residing near the base of subsequent diprotodontine radiations. Although Woodburne (1967a) does not make the point explicit, the odontological similarity of *Pyramios* with certain Alcoota zygomaturines is difficult to ignore, and some of the ambiguities in differentiating *Pyramios* from the zygomaturines are implicit in his conclusions.

Among the zygomaturines, some *Plaisiodon centralis* specimens have strong postparaconal crests, as in *Alkwertatherium*. The molar parastyles of both *Alkwertatherium* and *Plaisiodon* are relatively small; and the interloph valleys are proportionally similar in these genera. The thick, short labial cingulae that arise along the anterior ends of the midvalleys are also present in some *Plaisiodon* specimens and are especially prominent in *Alkwertatherium*.

Assuming monophyly for the Diprotodontidae, *Pyramios* and *Alkwertatherium* could represent remote descendants of the two respective subfamilies (Fig. 14). An alternative hypothesis is that *Pyramios*, *Alkwertatherium*, *Plaisiodon* and perhaps *Kolopsoides* represent an intermediate clade of diprotodontids into which a degree of parallel evolution (i.e. independent development of the parastyle and hypocone) must be introduced. The reality is, given the degree of morphological variability (ie. absence of hypocone in some *Neohelos* specimens) and difficulty in establishing clear complementary distributions in character complexes in these genera (correlation of the presence or absence of a feature with another), combined with the extraordinarily long period of time since their inferred divergence from a parent clade or their respective parent clades, that few "pristine" character states of a precisely comparable nature are present for comparison.

The cladogram (Fig. 14) is based primarily upon dental morphology, particularly the upper third premolar. The family Diprototodontidae is distinguished from the Palorchestidae on the basis of the synapomorphic loss, incorporation or suppression of stylar cusps C and D into the lophs (Fig. 14 [1]). The abscnee of the parastyle on the P^3 is plesiomorphic. A symplesiomorphic diprotodontid character is the presence of a large epitympanic fenestra, which decreases in size in the derived diprotodontids, but remains more highly expressed in the zygomaturines than in the nototheres. In *Pyramios* the epitympanic fenestra is small and simple (Woodburne 1967b) whereas in *Neohelos*, the fenestra is usually large, though sometimes subdivided and narrowed transversely. The ventral squamosal tympanic wing is virtually absent in plesiomorphic diprotodontids so that the tympanic cavity is a mere hollowing of the posterior wall of a bulla-like hypotympanic swelling that also forms the entoglenoid eminence. In *Pyramios*, a secondary ventral tympanic process is derived from the mastoid (Woodburne 1967b). The polarity of this morphological complex appears to be a progressive reduction of the alisphenoid tympanic process, present in *Propalorchestes* (Murray 1986) to a short, entirely squamosal tympanic process (e.g. Vombatidae). The diprotodontid conditon is accompanied by a hypertrophy of a hypotympanic sinus immediately anterior to the tympanic cavity and the tympanic process is further reduced. In *Pyramios*, the reduced anterior processes are replaced by a mastoid tympanic wing. In *Diprotodon* the tympanic cavity is partially floored by fusion and hypertrophy of other surrounding elements. In all known zygomaturines, except perhaps, *Zygomaturus*, in which secondary bony fusions are evident, the tympanic cavity is open ventrally.

The derived diprotodontids show a more distinct front to back molar gradient than in palorchestids and primitive diprotodontids (Fig. 14 [2]), (Rich *et al.* 1978). Plesiomorphically a strong paracristid (paralophid crest of Stirton *et al.* 1967) is present.

The synapomorphic basis for clade stem [3] is inferred to be the reduction of the paralophid crest on M^2. There is a plesiomorphic retention of the small parastyle, high mesostylar cusp and simple, undivided parametacone on the P^3.

Pyramios alcootense retained or developed a P^3 of large size relative to the molars [4] with a small, though in some individuals (SGM P872) an incipiently zygomaturine-like, parastyle. Symplesiomorphically the upper mo-

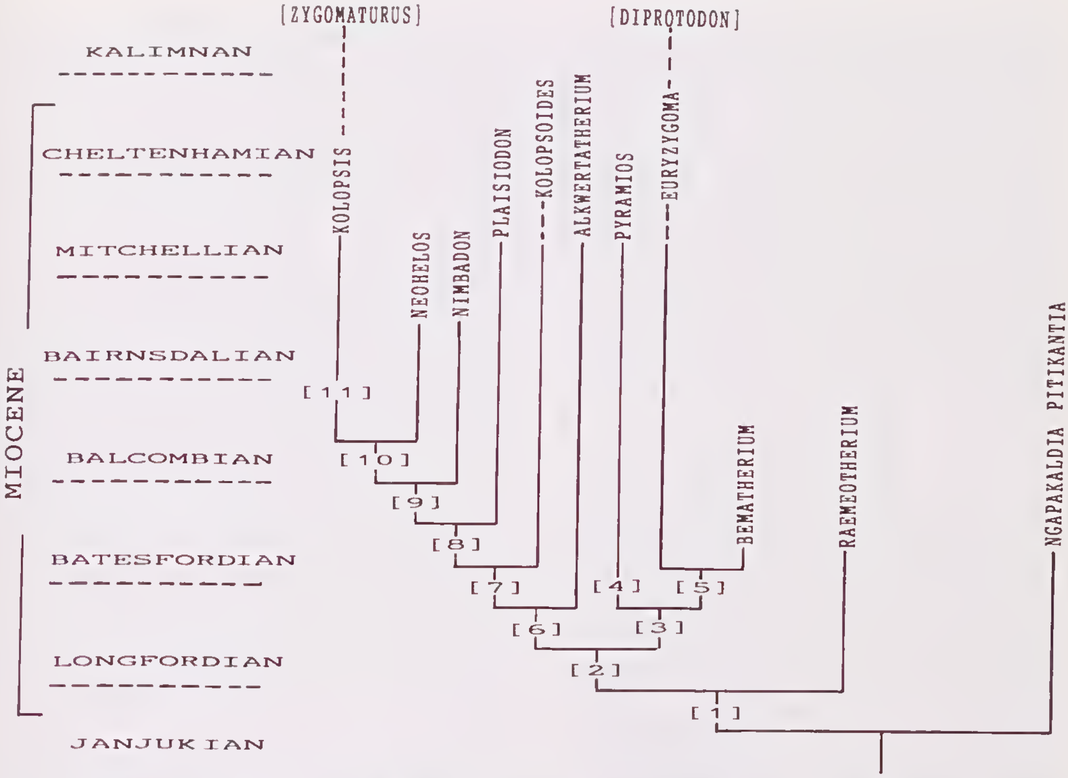

Fig. 14. Hypothesis of phylogenetic branching in Miocene diprotodontids based primarily upon a cladistic assessment of odontological characters (Table 5), depicted with minimum circuitry. The approximate Lyellian equivalency of the included genera is related to pan-continental stages (Woodburne *et al.* (1985). The discussion contains a more detailed interpretation. **[1]** loss, incorporation or suppression of stylar cusps C and D in relation to the lophs; **[2]** distinct front to back molar gradient; **[3]** reduction of paralophid crest; **[4]** P^3 large relative to molars; **[5]** reduction of size of permanent premolars relative to molars; **[6]** large parastyle, separated from the parametacone by a deep cleft; **[7]** development of a hypocone on the P^3; **[8]** "hook-like" parastyle on P^3 (Hand *et al.*, in preparation); **[9]** basic proportional similarity of the P^3 in *Nimbadon* and *Neohelos* (narrow posterior fovea of P^3, etc); **[10]** mesostyle retracted towards cingulum; **[11]** parametacone in *kolopsis* divided into two distinct cusps.

lars develop midlinks to the extent of *Plaisiodon* and *Alkwertatherium*. The paralophid crest is weak or absent and the protolophid of M^2 is high and steep.

Character complex [5] sets the other nototheriines apart from *Pyramios*: synapomorphic reduction of the size of the permanent premolars relative to the molars and tendency towards higher, steeper lophs and lophids.

The development of a large parastyle on the P^3 [6] unites all zygomaturine diprotodontids. Plesiomorphically it lacks a hypocone, is broad posteriorly and retains a high stylar cusp on the labial side of the apex of the parametacone. A marked narrowness of the metaloph relative to the protoloph on M^4 and especially M^5 is also characteristic.

Subsequent zygomaturines are united by the development of a hypocone on the P^3 [7]. Plesiomorphically the genus *Kolopsoides* retains a poorly differentiated parastyle, though interpreted by Plane (1967) to be a derived feature. Autapomorphically, the hypocone is as large or even larger than the protocone in *Kolopsoides*. *Kolopsoides* and *Plaisiodon* appear to be united by a lengthening of the parametacone in which however, the paracone and metacone remain essentially undifferentiated, the mesostylar cusp remains high and poorly defined labially, and a posterobuccal cingulum is absent in these two genera. Phenetic similarity in the long, nearly horizontal dentary symphysis of *Plaisiodon*, *Kolopsoides* and *Alkwertatherium* combined with the large, deep, almost fully enamelled lower incisors in (young only) *Kolopsoides* (Plane 1967) suggest a minor clade grouping, but evidence is thin.

Nimbadon and *Plaisiodon* are tenuously united by a "hook-like" shape of the parastyle of P^3 (Hand *et al.* personal communication) [8]. The shape and proportions of the cusps the P^3 are also similar in *Neohelos* and *Nimbadon* [9]. However, *Neohelos* usually has a prominent buccal cingulum with a small but fully differentiated mesostyle located well below the apex of the parametacone [10]. In *Kolopsis* the parametacone is divided into two distinct cusps [11] and an anterobuccal in addition to a posterobuccal cingulum, sometimes with a defined mesostyle, is usually present.

DISCUSSION

The similarities between *Alkwertatherium* and *Pyramios* on the one hand and *Alkwertatherium* and *Plaisiodon* on the other, are not easy to reconcile because of discontinuities in some of the character complexes and the continuously varying nature of others. My initial impression of *Alkwertatherium* was that it might belong to the genus *Plaisiodon*, (Murray 1989), impetuously resulting in a *nomen nudem* status for the name *"Plaisiodon" webbi*. Although the type *Pyramios* description seemed more remote relative to *Alkwertatherium* than that of *Plaisiodon*, there are also both general and specific similarities to *Pyramios*. In order to include *Alkwertatherium* within one or the other genus, either generic diagnosis would have to be revised to accomodate the specimen. If the differences among *Plaisiodon*, *Pyramios* and *Alkwertatherium* were to be sunk to the specific level, the subfamilial diagnoses as well as the generic diagnoses would require revision due to the higher level systematic emphasis placed upon the presence of a large, differentiated parastyle on the P^3 of *Alkwertatherium* and all other zygomaturines. The least disruptive option is to differentiate the new form at the generic level.

Alkwertatherium shows divisions of certain character complexes that are perceived as interrelated characters in other Alcoota genera. For example, the protolophid of M_2 is steep in *Alkwertatherium* but the paralophid crest is more differentiated than in *Pyramios*, suggesting that the two characters are genetically independent. The long, horizontal symphysial profile in *Alkwertatherium* is more similar to that of *Plaisiodon* than to the nearly vertical profile of *Pyramios*, yet the procumbent incisor implantation and morphology of the incisors suggest a closer relationship between *Pyramios* and *Alkwertatherium*. Conversely, the deep, spatulate lower incisor crowns of the zygomaturine *Kolopsoides* are more similar to those of *Alkwertatherium* and *Pyramios* than to those of other zygomaturines.

The constricted diastemal palate in *Alkwertatherium* is very similar to the condition in *Pyramios* and other nototheres. It is one of a few consistent apomorphic features that could unite the diprotodontinae (nototheres) and, were it not for the prominent parastyle-bearing *Alkwertatherium*, a monophyletic grouping might be supported with this character. *Plaisiodon centralis* also has a more extreme constriction of the diastemal palate than in other zygomaturines, except perhaps for *Zygomaturus*. The condition varies continuously from *Pyramios* to *Alkwertatherium* to *Plaisiodon* (Fig. 6). A number of other features (Table 5) align the cranium of *Alkwertatherium* to the zygomaturines, especially to that of *Plaisiodon*.

The zygomaturines *Nimbadon*, *Neohelos* and *Kolopsis* appear to form a distinct subclade, largely through a retention of plesiomorphic zygomaturine features. I surmise that they separated from the *Alkwertatherium-Plaisiodon-Kolopsoides* subclade at the point of the expression of the hypocone on the P_3. In order to express this phenomenon on a cladogram, I would be compelled to postulate a series of dichotomies for which there is no concrete evidence. A similar series of dichotomies would be entailed to resolve the relationship between *Pyramios* and *Alkwertatherium*. I have not expressed these palaeontologically unsupported branchings on the cladogram.

It has not been directly demonstrated in the fossil record that the zygomaturines arose from a parastyle-less ancestor. The condition is inferred from the plesiomorphic alignment of palorchestids with the diprotodontids. The earliest recognizeable diprotodontids (e.g. *Ngapakaldia*) lack the prominent parastyle of zygomaturines (Murray in press; Murray and Wells, in press).

The preferred hypothesis is that zygomaturines arose from a nototherc-like form in which the parastyle was reduced, as in primitive palorchestids. It is therefore more compelling to view *Pyramios* as a structural intermediate between the diprotodontines and zygomaturines, than to place the genus in a position ancestral to later diprotodontines. The morphology of *Alkwertatherium* is resolved as being largely symplesiomorphic with *Pyramios*, but in possession of the zygomaturine apomorphy of a large, differentiated parastyle.

As yet, there are no recognizable annectent forms for either *Alkwertatherium* or *Pyramios* in any of the pre-Cheltenhamian local faunas. The Bullock Creek *Neohelos tirarensis* appears to be closely related to *Kolopis torus* (Stirton *et al.* 1967). *Nimbadon* spp could represent basal zygomaturines with some specific affinity to *Plaisiodon* and *Neohelos* (Hand *et al.*, in preparation) but there is no firm evidence to support this observation. It is not likely however, that the apomorphic character complexes in *Alkwertatherium* and *Pyramios* evolved entirely within the intervening period between the mid- and late Miocene. It is reasonable to assume that the ancestors of both of these distinctive genera will eventually be recognized in one of the early to mid-Miocene faunas.

The presence of *Alkwertatherium*, *Plaisiodon*, *Pyramios* and other unique non-diprotodontid forms such as the primitive macropodid *Hadronomas puckridgi*, sets the Alcoota Local Fauna apart from the mid-Miocene and early to mid-Pliocene faunas. It appears to represent an assemblage of plesiomorphic relicts, the ancestors of some of which must antedate the Bullock Creek Local Fauna and which must have evolved in relative isolation. Of the diprotodontids, only *Kolopsis* is suggestive of later annectents (*Zygomaturus*). I suspect therefore, that a significant portion of the Alcoota Local Fauna may represent a relict of early to mid-Miocene radiations analogous to the New Guinea Pliocene local faunas. Although there is no obvious geographic feature that would explain such an isolation, it may be that the isolation of drainage patterns and associated habitats occurred earliest in the centre, severely limiting population movements by mid-Miocene times.

CONCLUSIONS

Alkwertherium webbi gen. et sp. nov. establishes a close relationship between diprotodontines (= nototheres) and zygomaturines, if it is accepted that *Pyramios* is a diprotodontine rather than a primitive zygomaturine. The Alcoota form, *Plaisiodon centralis*, appears to be more closely related to *Alkwertatherium* than to any other known zygomaturine. It is postulated that there were two minor zygomaturine lineages, one represented by *Nimbadon*, *Neohelos* and *Kolopsis*, and the other represented by *Alkwertatherium*, *Plaisiodon* and *Kolopsoides*. The two minor lineages could be united through the ancestor of *Nimbadon*.

This assumes, of course, that I have not described one of the extreme ends of two highly variable generic clines (*Plaisiodon* and *Pyramios*) as a new genus. I justify the generic distinction of *Alkwertatherium* on the basis of its possession of a character that is also employed to distinguish the two subfamilies of the Diprotodontidae. The systematic emphasis of this character depends upon the assumption that *Alkwertatherium* is more derived than *Pyramios* and more primitive than *Plaisiodon*. Should it eventually be shown that *Alkertatherium* is an extreme variant of either genus, this account would be no less informative, because it will have drawn attention to a degree of morphological variability sufficient to seriously question current diprotodontid systematics.

Meanwhile, I submit that *Alkwertatherium* accounts for some of the anomalies in the cheek tooth measurements of *Pyramios* and *Plaisiodon* provided by Woodburne (1967a). Its morphology, though derived, provides a glimpse of the antecedents of the two subfamilies of diprotodontids and gives some indication of the polarity of certain characters as well as documenting structurally, the stages transitional between diprotodontines and zygomaturines.

SUMMARY

Alkwertatherium webbi exhibits a unique combination of diprotodontine (= nototheriine) and zygomaturine characters in its cranium, dentition and dentary morphology. Although the upper third premolar had developed a large parastyle as in the zygomaturine diprotodonts, it retains a weak posterobuccal cingulum, lacks a hypocone and otherwise resembles the P_3 of the notothere, *Pyramios alcootense* Woodburne. The cranium of *Alkwertatherium* is basically similar to that of the

zygomaturine *Plaisiodon centralis* Woodburne, differing principally from that genus in having an extremely constricted diastemal palate, expanded interincisival fossa and incisor angulation more characteristic of nototheriines. The dentary resembles some nototheriines and especially palorchestines in having a long, narrow sublingual fossa and spatulate incisors, but is more similar to the zygomaturine *Plaisiodon* in overall shape and proportions. *Alkwertatherium* can be explained as a relict form which evolved from an ancestral clade structurally intermediate between zygomaturines and nototheriines. It is concluded that *Alkwertatherium webbi* is a late surviving representative of a plesiomorphic zygomaturine clade ancestral to *Plaisiodon centralis* and *Neohelos tirarensis*.

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